A RECONSTRUCTION OF STEPPE BISON MOBILITY IN THE YUKON-TANANA UPLANDS AND IMPLICATIONS FOR PREHISTORIC HUMAN BEHAVIOR

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A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

MASTERS OF ARTS

By

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Fairbanks, Alaska

August 2015

ABSTRACT

This study seeks to characterize steppe bison (*Bison priscus*) behavioral ecology in interior Alaska during the Pleistocene for the purpose of understanding how bison may have moved about the landscape on a seasonal basis and how this behavior could have influenced prehistoric human settlement and subsistence patterns. Steppe bison were present in Alaska and other circumpolar regions during the Pleistocene but became extinct during the late Holocene. Archaeological evidence from the Tanana River Basin in interior Alaska indicates that bison were an important component of human subsistence economies for at least 10,000 years, but aspects of steppe bison behavioral ecology including location of habitat area, seasonal movement patterns, and responses to environmental change remain largely unexplored in Alaskan archaeology or paleoecology.

This study applies strontium, oxygen, and carbon isotopic analyses to 14 sequentially-sampled and AMS radiocarbon dated steppe bison teeth from two locales in the Yukon-Tanana Uplands in order to reconstruct steppe bison behavior on a seasonal basis. This study is the first of its kind for any prehistoric species in Alaska, and the results indicate that steppe bison did not migrate great distances, but instead, moved between different ecotones seasonally, spending summers in higher elevation regions and winters in lower elevation regions. The results also indicate that steppe bison had greater mobility during periods of warmer climate, including Marine Isotope Stage 3 (MIS3) and during the Late Pleistocene.

Bison would have represented a large-bodied and predictable source of food for prehistoric peoples, and these results suggest that human landuse patterns likely incorporated the use of upland regions during the summer and fall, and lowland regions during the winter and early spring. Additionally, the results suggest that bison movement on the landscape would have

been more predictable during the Late Pleistocene than during the Holocene. As such, settlement and subsistence patterns may have shifted from a more residentially-organized pattern during the Late Pleistocene to greater logistical mobility during the Holocene as bison population became more mobile.

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ACKNOWLEDGEMENTS

This work would not have been possible without the support and encouragement of many people. I would foremost like to thank my committee members Ben Potter, Jamie Clark, Matthew Wooller, and Joshua Reuther. I am deeply grateful for the guidance, inspiration, and mentorship that they have provided during this process. Mat has taught me to look at the world through "isotope glasses", and his generous grant contributions funded the isotopic analyses in this thesis. Josh's enthusiasm for research and reconstructing the past world is contagious. He has been a constant source of encouragement and inspiration for not only this work, but for all research in general. I am especially grateful to my co-advisors Ben and Jamie for their support and encouragement of this project, even when it was little more than a rough idea. They have both taught me to think critically about the archaeological record, to structure research around theoretically-informed perspectives, and to ask the 'big-picture' questions. Ben's research in particular has provided a foundation for the theoretical application of this research, especially regarding past settlement and subsistence patterns in interior Alaska. Jamie's mentorship, regarding this thesis, as well as navigating grad school in general, has been immensely appreciated, and without her insightful comments this manuscript would have been much less coherent.

I would also like to thank Carol Gelvin-Reymiller for first introducing me to faunal analysis and for showing me how much information animal bones can contribute to the archaeological record. Carol emphatically told me that in order to learn how to identify bones you must *feel* them. I understand now that this did not mean physical touch, but rather a deeper meaning only gained from years of studying animal physiology and behavior. I will be forever grateful for the wisdom and love of animal bones that she imparted to me.

I would also like to recognize all those that contributed support for this research. Thank you to Pat Druckenmiller and Julie Rousseau from the University of Alaska Earth Sciences Department for permitting me to access the Lost Chicken Creek collection, and to the Army Core of Engineers for allowing me to have access to the CRREL specimen. Thanks to Darren Bruning and colleagues at ADF&G for providing me with the modern specimens and information about the Delta Bison Herd. A special thanks to Carrin Halfman for providing guidance about lab methods and showing me how to chemically process my samples. The strontium isoscape published by Clement Bataille and colleagues has provided an important component to this study; I would like to especially thank Clement for sharing the isoscape raster dataset with me. I am also grateful to the Harvey Shields Scholarship, the David and Rachel Hopkins Fellowship, and the Geist Fund, which have all provided funding for this research. I would also like to thank all of my fellow grad students who have been a constant source of support, encouragement, and inspiration over the past three years. I would particularly like to acknowledge my friends and cohort, Joe Keeney, Erin Dinneen, and Sharla Luxton, whose ridiculous group-texts, frequent trips to the pub, and constant laughter made even the roughest days enjoyable.

Finally, I would like to thank my family who has provided immeasurable support and encouragement, not only during these past few years, but throughout my entire life. To my parents, thank you for instilling in me an innate curiosity about the natural world and for encouraging me to always learn. To my sisters, thank you for constantly cheering me through this process and providing well-placed distractions when I most needed it. Lastly, I would like to thank my partner George, whose patience seemed endless as I navigated the tribulations of grad school, and for being the one that encouraged me to return for a graduate degree in the first place.

CHAPTER 1: INTRODUCTION

Steppe bison (*Bison priscus*) were present in Alaska and other circumpolar regions throughout the Pleistocene. They were an important species from both an ecological (e.g., Guthrie 1990) and an archaeological perspective (e.g., Potter et al. 2013b), yet biomolecular reconstructions of their behavioral ecology remain limited to a few studies that have either only addressed dietary reconstructions (e.g., Bocherens 2003; Fox-Dobbs et al. 2008) or focused on constrained temporal periods (e.g., Julien et al. 2012). While these studies have contributed to a greater understanding of steppe bison behavioral ecology as a whole, there still remains a large gap in our understanding of their behavior on a localized scale for Alaska, including whether they moved across the landscape on a seasonal basis, the types of physical locations that may have served as ideal habitat in the past, and how they may have responded to climate-based changes in the environment.

The goal of this research is to reconstruct the behavioral ecology of steppe bison from interior Alaska during the Late Pleistocene[1] (~50,000-11,500 BP[2]) in order to explore how bison behavioral ecology could have potentially structured prehistoric human behavior. Throughout prehistory, wherever humans and bison have coexisted on the landscape, bison have influenced countless aspect of human lifeways, including mobility patterns, settlement structure, economics, technology, ideology, and the transmission of knowledge (Arthur 1975; Bamforth 1987,1988; Barsh 1999; Barsh and Marlor 2003; Brink 2008; Frison 1991; Verbicky-Todd 1984). This suggests that reconstructing bison behavioral ecology in Alaska can be informative for modeling

[1]Late Pleistocene in the context of bison/environment refers to the period between the beginning of the last interstadial period (~57,000) and the beginning of the Holocene (~11,500 BP).
[2] Unless otherwise noted, all dates are presented as calibrated years before present (BP).

past human behavior in the region and can contribute to a more holistic understanding of past lifeways.

1.1 Setting the Stage: Background and Project Overview

It has been estimated that steppe bison made up as much as 50% of the biomass of Pleistocene mammalian communities in interior Alaska (Guthrie 1968), and steppe bison have been attributed with helping to maintain the unique steppe-ecosystem by stimulating plant growth, facilitating nutrient cycling, and maintaining grazing lawns which other species could have used and benefited from (Gates et al. 2010; Guthrie 1990). From a human perspective, bison were a key component of early subsistence economies and were used as a resource for over 10,000 years (e.g., Potter et al. 2013b; Stephenson et al. 2001). However, there are no naturally occurring herds of bison in Alaska today, and genetic reconstructions indicate that steppe bison became extinct during the late Holocene (~3,000 - 500 BP; Shapiro et al. 2004), although they may have been replaced with a descendant species known as wood bison (*B. b. athabascae*; Stephenson et al. 2001). Ethnographic information indicates that knowledge of bison and bison hunting still resides in the collective memories of Tanana, Gwich'in, and First Nations elders (Lotenberg et al. 1996; Stephenson et al. 2001), providing additional evidence that bison were an important subsistence resource throughout human prehistory in Alaska and adjacent regions.

Even though bison were important from ecological, archaeological, and ethnographic perspectives in interior Alaska, surprisingly little is known about their behavioral ecology on a local scale. Guthrie (1990) provided one of the most thorough reconstructions of steppe bison behavioral ecology when he wrote a monograph on the now-famous Blue Babe mummy. While this manuscript provides a wealth of information on paleo-environmental reconstructions and

animal behavioral ecology, many of the reconstructions of steppe bison seasonal movement patterns, herd structure, and habitat use were based on modern analogs (Guthrie 1990).

Modern wood bison and plains bison (*B. b. bison*) are directly descended from steppe bison and certainly provide the best-fit proxies for prehistoric behavioral reconstruction. However, research has demonstrated that modern bison behavior can be structured by numerous environmental factors, including temperature, precipitation, availability of forage and habitat, population densities, time of year, presence of predators or biting insects, or physical landscape (*c.f.,* Plumb et al. 2014). This indicates that reconstructions of prehistoric bison behavior based on modern bison population dynamics alone may be inadequate as climactic and environmental factors likely significantly influenced bison behavior in the past.

This study builds upon previous work that has emphasized the importance of understanding the behavioral ecology of the large prey species that were key components of prehistoric human subsistence economies (e.g., Britton 2009; Frison 2004; Graves 2009; Julien et al. 2012; Rivals et al. 2007; Widga 2006). Ethnographic evidence suggests that the behavior of key prey species likely influenced many human decision-making processes, and in order to more fully understand this relationship, it is necessary to reconstruct the behavioral ecology of those species (*c.f.,* Kelly 2013). This can provide information relating to aspects of human lifeways including subsistence strategies, seasonal mobility, site location and function, land-use, and risk management.

As gregarious herd animals, bison would have represented a large and predictable resource for human hunters Alaska. Identifying the mobility patterns of bison on a local scale can contribute to our understandings of how they were used by humans as a subsistence resource, and this information can then be used to develop expectations about how the seasonal movement

of bison may have affected settlement and subsistence patterns during the Late Pleistocene and Early Holocene.

1.1.1 Region of Study

The region of focus in this study is on Tanana Basin and Yukon-Tanana Uplands (YTU) which are both located in interior Alaska. This study region was chosen for two primary reasons; first, the Tanana Basin has some of the best preserved archaeological faunal material in interior Alaska, particularly for Late Pleistocene[3] and Early Holocene[4] sites, and there are hundreds of archaeological sites that span the entirety of human occupation from the Late Pleistocene through historic times and is also home to modern Athabaskan peoples as well. Due to exceptional faunal preservation at some of those sites, there have been concerted efforts focused on reconstructing prehistoric subsistence behaviors (e.g., Holmes 2011; Krasinski and Yesner 2008; Potter 2005; Potter et al. 2013a, 2013b; Yesner 1996; Yesner et al. 2011), and this research has demonstrated that steppe bison were an important resource in this region during the Late Pleistocene and Early Holocene. Second, the Tanana Valley and YTU have yielded hundreds of paleontological specimens of steppe bison from stratigraphic deposits dating to multiple different climatic periods during the Late Pleistocene. This suggests that the region provided habitat and forage for bison herds for at least 100,000 years and was part of the 'bison belt' that stretched from Siberia to Canada during the Pleistocene (Guthrie 1990).

The Tanana basin and YTU encompasses a large portion of interior Alaska. The Tanana Valley lowlands include an area of about 18,000 km^2 beginning at the confluence of the Nabesna and Chisana rivers where the Tanana begins its course, before flowing through a wide valley and

[3] Late Pleistocene in the context of humans refers to the period of human occupation between 14,000-11,500 BP.
[4] Early Holocene refers to the period between ~11,500-6,000 BP.

emptying into the Yukon River for a total length of ~400 km (Mason and Beget 1991). The Tanana River is primarily glacier fed, and this has allowed for deposits of thick silt and loess to accumulate throughout the valley, providing excellent stratigraphy for many sites. The river valley is bounded and fed by the Alaska Range to the south which supplies around 85% of the watershed and the YTU to the north, which provide about 15% of the watershed for the Tanana River (Yarie et al. 1998). The Alaska Range is a rugged region with high relief, glaciated areas, and strong winds that frequently sweep into the Tanana Valley. Comparatively, the YTU are geologically older, providing a more weathered upland area with less vertical relief and more vegetation and habitat area for modern game animals.

1.2 Research Questions

This study focuses on four primary questions:

1) *Were steppe bison seasonally migratory in the past?*

The goal of this question is to understand whether steppe bison moved about the landscape and whether seasonal migration occurred. In this thesis, the terms migratory and mobility are used synonymously to mean 'movement on the landscape'. It should be emphasized that use of either term does not inherently mean a large-scale change in geographical location, but can simply refer to localized use of the landscape (over a few kilometers), or can refer to greater distances over multiple regions or ecotones (in the scale of hundreds of kilometers). The purpose of this study is not to quantify precise distances traveled by bison, but rather to understand whether there is evidence for change in physical location on a seasonal basis, and if possible, to estimate range size.

2) *Can bison be associated with certain geographical variables on the landscape?*

This question seeks to identify whether there are specific habitat areas, waterways, or landforms that can be associated with steppe bison. The goal is not to suggest a dichotomous relationship between the presence/absence of bison in certain areas, rather to determine whether there may have been certain physical locations that would have been more heavily used by bison populations in the past. This information would have important implications for the archaeological record, including predicting the location of sites, understanding the season of occupation, modeling hunting and subsistence patterns, and reconstructing human mobility patterns on the landscape. A greater understanding of the factors that influenced archaeological site location in the past could also benefit cultural resource management practices and ensure greater protection of archaeological sites.

3) *Did bison mobility patterns change through time?*

This study also aims to explore if and in what ways bison mobility may have changed through time. This can be informative for understanding how climate and vegetation changes during the Late Pleistocene and Holocene may have affected bison populations. If bison mobility patterns demonstrate no change through time, it can be assumed that environmental change had little effect on their behavioral ecology. However, if there are indications that mobility patterns changed over time, this may provide a line of evidence that climate change altered their behavioral ecology. This information could potentially inform on modern management practices and understandings of species-specific responses to climate change.

4) *How could bison mobility have potentially structured prehistoric subsistence & settlement patterns?*

The ultimate goal of this study is to address how bison behavior may have influenced prehistoric human populations. The assumption is made that bison mobility patterns would have structured human settlement and subsistence behavior to some degree during the Late Pleistocene and Early Holocene. Specifically, if bison migrated between different regions on a seasonal basis, then settlement and subsistence patterns may have been organized around the seasonal behavior of these animals, and this relationship may have been reflected by high residential mobility for human populations. Conversely, if bison stayed in one region throughout the year, then they would have represented a predictable resource which would have been available in any season, and residential sites likely would have been occupied for longer duration and residential moves would have likely been less-frequent.

These four questions are addressed through isotopic methods, specifically, through strontium ($^{87}Sr/^{86}Sr$) oxygen ($\delta^{18}O$) and carbon ($\delta^{13}C$) isotopic analyses (these methods are discussed in Chapter 4). Ungulates have unique dentition from other mammals in that the enamel portion of their teeth grows in sequential layers; as a tooth forms, those sequential layers trap isotope values from specific periods of the individual's life. In bison, the second and third molars form over the first 1-3 years of life; during that formation period, isotopic input from the surrounding environment will be trapped in the dental enamel (Gadbury et al. 2000). By taking sequential samples down the transverse plane of a bison molar, changes (in the isotope values) over time within an individual can be identified.

Strontium isotopes have geographical variation that can be associated with physical locations on the landscape (*c.f.,* Bentley 2006) and $\delta^{18}O$ values can demonstrate seasonal and altitudinal variation (e.g., Fricke et al. 1998; Gat 1996). Therefore, by analyzing individual serial-samples for $^{87}Sr/^{86}Sr$ and $\delta^{18}O$ removed from a bison tooth, change in geographical location on a seasonal basis can be investigated (*c.f.,* Julien et al. 2012). Oxygen and carbon isotopes can also be used as a proxy for past environment and season (e.g., Marshall et al. 2007), and are used in this study to help identify environmental and seasonal factors.

Isotopic ratios were analyzed on a total of 106 individual samples removed from 14 prehistoric steppe bison teeth from two locales in the YTU, including the CRREL permafrost tunnel and Lost Chicken Creek. A recently-published strontium isoscape for the state of Alaska (Bataille et al. 2014) was used to compare the specimen $^{87}Sr/^{86}Sr$ values with actual physical locations on the landscape, and was integral to interpreting the results of this study. However, the isoscape did not predict the $^{87}Sr/^{86}Sr$ values in the YTU as accurately as in other regions of the state (Bataille et al. 2014). This issue, combined with the fact that $^{87}Sr/^{86}Sr$ values in riverine systems can vary on a seasonal basis in regions of permafrost (Douglas et al. 2013), and the fact that this study is the first of its kind for any prehistoric species in Alaska, made it necessary to also incorporate a modern control study. The modern study applied the same sampling and analytical method to three bison teeth from the Delta bison herd, which resides near Delta Junction in the Tanana Valley. The Delta bison herd has well-known seasonal migratory patterns that provided the opportunity to evaluate 1) how well the isoscape (i.e., Bataille et al. 2014) performed for that region, 2) whether there were apparent seasonal influences in the $^{87}Sr/^{86}Sr$ signatures in bison teeth, and 3) more broadly, whether these methods would be effective for characterizing prehistoric bison behavioral ecology.

1.3 Organization of This Study

This thesis is divided into nine chapters. Chapter 2 describes the history of bison in Alaska, including paleontological, ecological, ethnographic, and archaeological information about bison. Chapter 3 discusses two different theoretical perspectives that have helped structure this study. The first perspective is based on the Principle of Actualism which contributes to theoretical considerations for the reconstruction of bison behavior. Information from modern bison herds is also discussed, as this information provides expectations about how prehistoric bison may have behaved. Human Behavioral Ecology (HBE) is also discussed in Chapter 3 as this theoretical framework provides several expectations about how humans may have organized their settlement and subsistence patterns around the seasonal movement of prey species, as well as theoretical considerations associated with behavioral responses to environmental risk and uncertainty. Chapter 4 provides background information on the methodological approaches that were used in this study, and explains how $^{87}Sr/^{86}Sr$, $\delta^{18}O$, and $\delta^{13}C$ isotopic signatures can be used to reconstruct the behavior as well as environmental context of biological organisms. Chapter 5 discusses the sample dataset, sample locales, sample collection and preparation methods, and the AMS radiocarbon results. Chapter 6 describes the modern control study, and provides background information on why a modern control study was considered necessary. Chapter 7 discusses the results, including the reconstructions of seasonal migratory behavior, change over time, and environmental context. Chapter 8 contextualizes the results in terms of human landuse patterns and discusses how bison behavior may have influenced human behavior. Chapter 9 concludes this thesis and summarizes the objectives, results, and implications of this study, as well as potential future directions.

CHAPTER 2: HISTORY OF BISON IN ALASKA

There are no naturally occurring herds of bison in Alaska today, but they were once an essential component of the steppe ecosystem and served as an important subsistence resource for prehistoric peoples for thousands of years. Steppe bison inhabited Alaska for over 100,000 years, and have been heralded as a 'keystone' species that would have facilitated grazing lawns, helped to maintain plant biodiversity, stimulate nutrient cycling, and create habitat area for other species (*c.f.,* Gates et al. 2010; Guthrie 2001; Zimov et al. 1995). Additionally, as gregarious animals that maintain a herd social structure, bison would have presented a predictable and abundant subsistence resource for prehistoric peoples (e.g., Bamforth 1987, 1988; Frison 1991).

Evidence of bison exploitation is found throughout Alaska (*c.f.,* Kunz et al. 1999), but especially in faunal assemblages from the Tanana Basin, which has a high density of sites dating to the Late Pleistocene and Early Holocene (e.g., Potter et al. 2013b). Evidence for bison exploitation during the middle Holocene (~7,000-3,000 BP) is limited, but ethnographic information shared by Athabaskan elders indicates that bison were an important subsistence resource as recently as one or two hundred years ago (Lotenberg et al. 1996; Stephenson et al. 2001). Together, the archaeological and ethnographic evidence suggest that for most of human prehistory in Alaska, bison were important to subsistence economies as a source of both food and raw material.

The history of North American bison, along with ecological, archaeological, and ethnographic information on steppe bison is discussed in this chapter. Research on modern bison indicates that the environment plays a large role in their behavior (e.g., Plumb et al. 2014); because of this factor, an overview of the environmental changes that have occurred in interior Alaska during the last ~50,000 years is also included.

2.1 Bison of the Steppes, Bison of the Woods

Steppe bison were one of the most prevalent megafaunal specie during the Pleistocene, and genetic reconstructions (Shapiro et al. 2004) and paleontological deposits (Guthrie 1968) indicate that they had migrated into Alaska by 130,000 years ago. Steppe bison were larger than their modern counterparts and evolved from an earlier bovid ancestor on the cool, dry, and windy Eurasian steppes during the middle Pleistocene (Guthrie 1970). The abundance of bison remains found in paleontological and archaeological contexts throughout Eurasia and North America has led researchers to suggest that bison made up a large portion of the biomass, forming huge herds that roamed across the land and helped to maintain the unique steppe ecosystem (Guthrie 1990; Zimov et al. 1995).

Steppe bison seem to have been especially abundant in interior Alaska towards the end of the Pleistocene, and Guthrie (1968) estimated that they many have represented as much as 50% of the biomass for unglaciated regions in the interior. Estimates for other regions have suggested that they represented smaller percentages of the biomass; Matheus (2003) estimated that bison represented approximately 35% of the biomass for the North Slope, while Mann et al. (2013) estimated about 23% for the same region. However, considering the diverse suite of fauna that inhabited Alaska during the Pleistocene, these lower estimates still indicate that steppe bison were the most abundant species during this time (Guthrie 1990). Steppe bison remains are also found in high abundance in archaeological sites dating to the Late Pleistocene and Early Holocene, until approximately 7,000 BP (Potter et al. 2013b), providing further evidence that they were abundant during that period as well as previous periods.

Steppe bison became extinct in Alaska and northern Canada during the late Holocene (~2,000-1,000 BP; Shapiro et al. 2004). The reason for the disappearance is not well understood,

although environmental change and genetic instability are thought to be major factors (i.e., Guthrie 2006; Shapiro et al. 2004). Hunting pressures from increased human population or the introduction of more effective hunting technology in the form of the bow-and-arrow around 1,000 BP, has also been suggested as a final catalyst that may have pushed already unstable populations to extinction (Gardner and DeGrange 2003; Potter 2008b; Stephenson et al. 2001). Although the understanding of late Holocene bison genetics in Alaska is limited (e.g., Shapiro et al. 2004), wood bison (a descendent subspecies of steppe bison) repopulated northern Canada during the Middle Holocene and may have repopulated Alaska after the extinction of steppe bison, although this remains unclear. Regardless of whether wood bison repopulated Alaska or not, there are no naturally occurring bison species in Alaska today, but there are several transplanted herds of both plains and wood bison that have adapted to interior boreal, mixed meadow, and riverine environments, suggesting there is still adequate habitat and forage for bison in Alaska (Alaska Department of Fish & Game 2015).

2.1.1 Phylogenetic History of North American Bison

Genetic reconstructions indicate that steppe bison first migrated into Alaska from Siberia sometime between 300,000-130,000 BP, and then spread throughout western Canada and into most of North America (Meagher 1986; Shapiro et al. 2004). Up until the Last Glacial Maximum (LGM) which began around 29,000 BP (Lisiecki and Raymo 2005), steppe bison appear to have thrived in North America with relatively unrestricted gene flow (Shapiro et al. 2004). However, glacial expansion in Canada during the LGM created a physical barrier that restricted gene flow between northern and southern populations; eventually, the clades south of the ice sheets evolved into a distinctive ancestral haplotype to modern North American bison,

known as *Bison antiquus* (Potter et al. 2010; Shapiro et al. 2004). This species spread throughout the southern portion of North America, and began spreading north, ultimately repopulating the once-glaciated regions of Canada during the Holocene. By 5,000 years ago, plains bison and woods bison had diverged from this ancestral population (van Zyll de Jong 1993; although there is argument as to whether they should be considered subspecies [*c.f.,* Boyd et al. 2010]). Plains bison adapted and thrived on the open prairie environment of the North American Great Plains and wood bison adapted to boreal environments in higher latitudes.

The northern clade of steppe bison remained in Alaska throughout the Pleistocene and appears to have been present until the late Holocene. The last unequivocal evidence (i.e., DNA sequencing) of steppe bison is from a paleontological specimen from the Black River region in the Yukon Basin and dates to ~2,300 BP (Shapiro et al. 2004). However, without ancient DNA (aDNA) analysis, it is often difficult to identify faunal remains to a subspecies level. Wood bison also inhabited western Canada during the late Holocene and may have spread into Alaska; however, there is no evidence of genetic admixture between steppe bison and wood bison, suggesting that wood bison did not enter northern regions until after steppe bison became extinct (Gates et al. 2010; Shapiro et al. 2004). It is accepted that bison remains in archaeological sites in Alaska represent steppe bison (*c.f.,* Potter et al. 2013b), although there remains a possibility that some of the faunal materials could actually be wood bison.

Interestingly, the northern clade of steppe bison (those in Alaska) became extinct as the southern clade (those south of the Cordilleran ice sheets during the LGM) evolved into a different species. The reason for the northern clade's evolutionary disappearance is not well understood; however, as previously mentioned, it is thought that habitat fragmentation and genetic instability played a large part in the extinction of northern steppe bison (e.g., Guthrie

1990; Shapiro et al. 2004). Reconstructions of *Bison priscus* genetics indicate that during the Pleistocene there were several expansions and contractions in gene flow. Shapiro et al. (2004:1564) analyzed aDNA from 442 bison fossils (>50% AMS dated) and demonstrated that preceding an "exponential" expansion in bison populations prior to 50,000 BP, there was a rapid decline in genetic diversity around 37,000 BP. The analysis indicated that between ~75,000-40,000 BP, bison populations were rapidly expanding, with an estimated doubling in population size every 10,000 years. However, between 42,000-32,000 BP, there seems to be a reversal of this trend with a "dramatic decrease in population size…coincident with the warmest part of the [last interstadial]" (Shapiro et al. 2004:1564).

Interestingly, this decrease in steppe bison population size coincides with the period of when forests nearly reached their present distribution in eastern Siberia and Alaska (Anderson and Lozhkin 2001). Guthrie (1990) noted that forests create barriers and lack of grazing habitat for modern bison, suggesting that the decline in genetic diversity between 42,000-32,000 BP may have been the result of habitat fragmentation, lack of forage, rapid shifts in the vegetation regimes, or other factors relating to environmental change. Based on aDNA analyses, steppe bison populations also appeared stressed during the LGM, even though habitat area and grazing vegetation appear to have expanded during this time (e.g., Guthrie 1990). Shapiro et al. (2004) argues that this was the cause of genetic bottlenecking during the last interstadial period which created too much population instability for bison populations to fully recover before the rapid climatic fluctuations that occurred during the Pleistocene-Holocene transition.

The current aDNA evidence suggests that bison populations flourished during cooler and dryer periods and became less stable during warmer periods of forest expansion (Shapiro et al. 2004). This same pattern is also reflected in the genetics of other Pleistocene species, and

climatic fluctuations during the last interstadial and glacial periods caused large-scale population instability for most of the carnivore and herbivore guild. There is evidence of population bottlenecks for at least five other steppe species between 50,000-15,000 BP, including saiga antelope (*Saiga tatarica*; Campos et al. 2010a), muskox (*Ovibos moschatus*; Campos et al. 2010b), brown bear (*Ursus arctos*; Barnes et al. 2002), mammoth (*Mammuthus primigenius*; Barnes et al. 2007), mastodon (*Mammut americanum;* Zazula et al. 2014) and lion (*Panthera atrox*; Barnett et al. 2009). Lorenzen et al. (2011) also argues that climate change was the driving factor for declines in genetic diversity for mammoth (*Mammuthus primigenius*), woolley rhinoceros (*Coelodonta antiquitatis*), horse (*Equus* ssp.), caribou (*Rangifer tarandus*), bison (*Bison priscus*) and muskox (*Ovibos moschatus*) over the past 50,000 years. This evidence suggests that the entire Pleistocene food web experienced rapid shifts during the late Pleistocene which may have been related to a bottom-up shift in vegetation communities.

2.1.2 Archaeological Evidence of Bison Use in the Tanana Basin

Humans first migrated into North America at the end of the Pleistocene, and based on site density and distribution, quickly expanded across the new landscape, adapting their subsistence strategies to the locally available fauna and following a pattern of broad-spectrum foraging (e.g., Yesner 2001). For over 6,000 years, bison and wapiti were the primary subsistence resource in the Tanana Valley, but were supplemented by small game, waterfowl, and some fish (Potter et al. 2013b; Yesner 2001; Yesner et al. 2011). However, between 8,000-5,000 BP there seems to have been a shift in subsistence economies, and bison and wapiti remains nearly disappear from the faunal record, and are replaced with caribou and moose faunal remains for the remainder of the Holocene (Potter 2008a, 2011; Yesner 1989). This shift in subsistence patterns suggests that

bison and wapiti populations either crashed around this time, or that those populations were not large enough to support frequent hunting. However, evidence for bison hunting continues later into the Holocene in the Yukon as bison remains have been found at sites dating to 3,000 BP (Farnell et al. 2004; Morlan 1977; Workman 1978).

Interestingly, oral history shared by Native elders in Alaska indicate that bison were an important subsistence resource within the past few hundred years (Lotenberg 1996; Stephenson et al. 2001), making the lack of bison remains in late Holocene assemblages somewhat enigmatic. While the conspicuous absence of bison remains suggests a sampling or identification bias, there are also two taphonomic factors that could be contributing to this issue. First, there were low rates of sediment accumulation and high soil acidity after about 6,000 BP due to the spread of the boreal forest (e.g., Dilley 1998; Gilbert 2011), which creates a poor preservation environment for organic materials (e.g., Arundale et al. 1989). The second factor is that resource intensification increased towards the end of the Holocene and faunal materials were processed to a much higher degree, making it difficult to identify fragmentary elements to the species level (e.g., Holmes 1986; Yesner 1989). Due to these two factors, reconstructing subsistence economies based on faunal materials is difficult for the latter half of the Holocene.

Both the archaeological and ethnographic evidence suggests that bison were an important subsistence resource throughout most of human prehistory in Alaska. However, bison remains especially dominate faunal assemblages during the Late Pleistocene and Early Holocene in the Tanana Basin at sites like Broken Mammoth (Krasinski and Yesner 2008; Yesner 2001), Mead (Potter et al. 2013a, 2013b) Gerstle River (Potter 2005, 2007) and Little John near the Alaska-Yukon border (Yesner et al. 2011). Potter (2011) also noted that there is evidence of different upland/lowland site use, and that at high elevation sites, such as those in the Alaska Range, the

faunal materials represent a narrower range of species, while sites in low elevation areas such as the Tanana Basin contain a much wider breadth of faunal materials including both large and small game. Additionally a majority of Late Pleistocene and Early Holocene lowland sites contain bison and wapiti remains (Potter 2008a, 2008c). Potter (2011) and colleagues (Potter et al. 2013b) emphasize that bison and wapiti were integral parts of the prehistoric subsistence base, and that human mobility patterns, seasonal resource scheduling, site locations, and settlement organization were likely structured around the seasonal availability and movement patterns of these large ungulates. While the majority of bison faunal remains are found in Late Pleistocene and Early Holocene sites, oral history tells a story of more recent bison use, and this information is discussed in the following section.

2.1.3 Ethnographic Information on Bison from Alaska and the Yukon

In the 1990s, interest in reintroducing and effectively managing wood bison populations in Canada and Alaska prompted researchers to record traditional Athabascan knowledge about bison and bison hunting (Lotenberg 1996; Stephenson et al. 2001). While this thesis is focused on reconstructing the behavioral ecology of steppe bison during the Late Pleistocene and Early Holocene, the ethnographic data still significantly contributes to a greater understanding of the importance that bison held as a subsistence resource for Native peoples, and also suggests that bison were present in Alaska and the Yukon and hunted throughout the Holocene, even though archaeological evidence for bison presence is limited.

Lotenberg (1996) recorded information from dozens of elders from Tagish, Dena, Selkirk, Tlingit, and Gwich'in First Nations in the Yukon, and led her to suggest that bison likely disappeared from the region within the last 400 years. McClellan (1975) had previously noted

that Teslin elders said that the last bison was killed when their grandparents were children, suggesting that bison may have been present in some regions of the Yukon within the past 200 years. The ethnographic information that Lotenberg (1996) recorded was not extensive, but did indicate that bison were an important component of the subsistence base in the past. Many of the elders noted that when bison were abundant, there were no trees on the landscape, and that moose did not spread into the country until after bison had disappeared. Traditional knowledge also indicated that bison would seek out windblown areas for grazing in the winter, which suggests that bison may have been utilizing low foothills and higher elevation areas as part of their seasonal habitat area (Lotenberg 1996).

Interest in reintroducing wood bison to Alaska also spurred Stephenson et al. (2001) to record traditional knowledge from Gwich'in and Tanana elders, and the information that was compiled suggests that bison were present in Alaska more recently, likely within the past 200 years. All of the elders that were interviewed differentiated between bison and other large ungulates, and many of them indicated the traditional name for bison, including *Dachantèe aak'ii/qwaak'ii* (cow in the forest/the hefty one among timber) or *Ch'itthay dighan* (humped meat) or *Nan'aak'ii choo* (big hefty one on the land), providing further evidence that bison were present on the landscape in the very recent past (Stephenson et al. 2001).

There were many similarities in the oral traditions from both Alaska and the Yukon, including that bison populations were substantial in the past and were extensively hunted as a source of food and raw material, that moose and other game were scarce when bison were abundant, that bison were hunted with bow and arrow technology, and that after bison populations declined trees and shrubs expanded as a result of bison no longer maintaining grazing areas (Lotenberg 1996; Stephenson et al. 2001). One conflicting piece of information

was where bison habitat was located, with Yukon elders indicating that bison used high elevation areas in the winter, and Alaskan elders indicating that bison were primarily located in low elevation areas in all seasons. However, this conflict of information may be due to seasonal, landscape, or herd-specific differences in bison behavioral ecology.

Gwich'in and Tanana elders in Alaska indicated that many of the oral traditions had been passed down through several generations, which suggests that bison may have held cultural as well as economic importance. Bison were said to provide "high quality" food and raw materials, including hides that were used for clothing and shelter and bones and horn that were used for tools and implements (Stephenson et al. 2001:129). The Reverend David Salmon, a renowned Gwich'in elder, reported that bison were once an important food source, emphasizing that "[his ancestors] lived on it" and that the Yukon River flats "is their [bison] country…they belong to it" (Stephenson et al. 2001:130). Moses Cruikshank, another respected Gwich'in elder, also recounted stories of a time in the past when large herds of bison roamed the Yukon flats and each fall dozens of bison would be killed by herding them over cliffs by using *inuksuit* (drive-lines), and then the meat and hides would be processed and stored for winter use (Stephenson et al. 2001).

While there is only one recorded account of communal bison hunting in Alaska, it is still interesting to consider from a heuristic perspective. Communal bison hunting with drive-lines, pounds, and jumps were often used by First Nations tribes such as Blackfoot, Cree, Assiniboine, and Gros Ventre (among many), and bison mass-kill sites have been identified dating to throughout the Holocene and stretching from northern Alberta to Mexico (*c.f.,* Arthur 1975; Bamforth 1987, 1988; Frison 1991, Barsh and Marlor 2003). Traditionally, bison hunters on the northern Plains would congregate during the fall rut when the largest bison herds would form,

and the animals would be driven into enclosures or over cliffs and killed (Arthur 1975). Large numbers of bison would be harvested this way, and then butchered and dried and stored for winter use (Arthur 1975). While there is limited ethnographic evidence (and currently no archaeological evidence) that bison were communally hunted in Alaska, it is interesting to note that caribou were harvested in a very similar manner. Like bison, caribou would be intersected on their annual migrations and driven into enclosures where dozens of animals would be harvested and processed for food and hides in preparation for winter use (e.g., McKennan 1965; West 1963). Many *inuksuit* have been identified in the Yukon, Porcupine, and Crow River regions (McKennan 1965; Vuntut Gwitch'in First Nation and Shirleen Smith 2009; West 1963). It has been assumed that the *inuksuit* were used for caribou hunting, but the drive-lines are often difficult to date, and considering that the Yukon Flats and tributary rivers were described as being prime bison habitat (Stephenson et al. 2001), it is possible that some of the *inuksuit* in the region could have been used for bison hunting as well, although this remains to be tested.

The majority of reported placenames, such as Buffalo Shirt Mountain near the Sheenjek River (reportedly gaining the moniker when a huge herd of bison "covered the mountain like a shirt"; Moses Cruikshank *in* Stephenson et al. 2001:131), were located in the Yukon River basin and surrounding tributaries. This led Stephenson et al. (2001) to suggest that this region may have been the last refugia for bison in Alaska. However, a few placenames were also reported for the Tanana Basin, including Minto Flats and the Chatanika, Good Pasture, and Fortymile Rivers (Stephenson et al. 2001). This suggests that bison may have disappeared or migrated out of the Tanana River basin at an earlier date, but not so long ago that knowledge of bison in the region had faded from living memory. Stephenson et al. (2001), as well as many of the elders who shared stories and knowledge about bison, estimate that bison were present in Alaska until

at least 200 years ago and possibly later as many of the accounts of bison sightings occurred in the early 20th century.

2.2 Previous Reconstructions of Steppe Bison Behavioral Ecology

Even though steppe bison were clearly important from both an ecological and archaeological perspective, there has been limited research that has sought to directly reconstruct their behavior. One of the most in-depth reconstructions was undertaken in the summer of 1989 when the carcass of a frozen steppe bison was uncovered near Fairbanks. Ecologist Dale Guthrie published a monograph on steppe bison behavioral ecology based on the frozen remains, known paleontological distribution of steppe bison, modern bison analogs, and other environmental data (Guthrie 1990). Guthrie inferred a variety of behavioral traits based on size, sexual dimorphism traits, pelage, and social organs (i.e., horns), including that steppe bison likely experienced an increase in agnostic behavior and group size during the Pleistocene, and were highly nomadic with a lack of homeland fidelity. He additionally suggested that steppe bison had a polygamous social structure similar to modern bison, and that females and juveniles lived in large herds while smaller groups of males lived peripherally to the large herd. Based on tooth wear patterns as well as identifications of plant remains trapped in the infundibulum of molars, Guthrie suggested that steppe bison were non-selective feeders and winter diets included high percentages of fiber. Using environmental reconstructions as a proxy, he determined that forage would have yielded low nutrition in the winter, which would have kept the bison populations below the summer carrying capacity (Guthrie 1990). This reconstruction remains one of the most thorough to date, and provides a wealth of information on modern and paleo-bison behavior.

Based on macro and microscopic analysis of dental wear patterns, steppe bison appear to

have consumed different diets than modern North American bison. Rivals et al. (2007) reconstructed the diets of four populations of North American steppe bison, and found a diversity of wear patterns which more closely resembled the wear patterns of modern mixed-feeding ungulates, rather than obligate grazers. The results suggested that the diets of the paleo-populations were more diverse as well as significantly less abrasive than the diets of modern plains bison, and in fact, the abrasion patterns for the paleo-population were similar to abrasion patterns on modern wood bison teeth (Rivals et al. 2007). Wood bison often incorporate browse into their diet during certain times of the year (Meagher 1986), which lead Rivals et al. (2007) to suggest that steppe bison consumed browse, at least during certain times of the year. Guthrie (1990) also suggested that steppe bison may have consumed greater portions of woody vegetation during the winter and during interstadial periods when there was a spread of woody vegetation, indicating that steppe bison diet and forage availability may have been more similar to the diet of wood bison than plains bison.

Applying similar methods, Rivals et al. (2010) also looked at dental wear patterns on a suite of ungulate species dating to the Late Pleistocene, including steppe bison. The wear patterns were described as being "ecologically bizarre" and did not resemble any known patterns in modern grazing or browsing species (Rivals et al. 2010:42). The dentition for all of the species was typified by rounded mesowear, indicating a highly abrasive diet. However, microscopic analysis showed many fine and narrow micro-scratches, which is atypical of modern ungulates that consume abrasive diets. Rivals et al. (2010) suggested that the wear patterns indicated a homogenous diet during the winter which may have included consuming large quantities of *Equisetum* or other plants near the ground such as lichen and mosses. The authors additionally noted that the two species with the most atypical dental wear patterns, *Rangifer* and

Alces, survived the Pleistocene extinctions, while the species that had patterns more similar to their modern counterparts, *Bison* and *Equus*, became extinct (Rivals et al. 2010). This suggests that steppe bison may have been constrained by certain dietary niches, and did not change their dietary behavior during the Pleistocene-Holocene Transition.

Diet choice for steppe bison has also been directly addressed using stable isotope analysis. Fox-Dobbs et al. (2008) reconstructed dietary niche-partitioning for several herbivore species from interior Alaska via $\delta^{13}C$ and nitrogen ($\delta^{15}N$) stable isotope analysis of bone collagen. The results showed two significant dietary shifts for all species which occurred between interstadial (50,000-25,000 BP) and full glacial times (25,000-18,000 BP) and between full glacial and post glacial times (e.g., >18,000 BP). The shifts in diet likely resulted from environmental changes which forced herbivore species to change or adapt their foraging behaviors (Fox-Dobbs et al. 2008). Additionally, the inter-species comparisons of the isotope values showed significant differences (except for *Equus* and *Bos*), indicating that there was dietary niche partitioning amongst the herbivore guild. The results suggested that *Rangifer* and *Ovibos* shared separate niches from other herbivores, *Equus* and *Bos* had slightly overlapping niches, and *Bison* and *Mammuthus* occupied a slightly different niche from all of the other species (Fox-Dobbs et al. 2008; see Figure 1 for graphed mean herbivore $\delta^{13}C$ and $\delta^{15}N$ values).

This suggests that while steppe bison likely did not have competition for food sources from other herbivore species, they may have been constrained by a limited choice of food sources or habitat area. Mann et al. (2013) also reconstructed the diets of several Pleistocene herbivore species from the North Slope of Alaska via $\delta^{13}C$ and $\delta^{15}N$ analysis of bone collagen. The results showed significant differences in the food sources of browsing and grazing herbivore species, but there was some overlap between *Bison* and *Ovibos* and between *Mammuthus* and

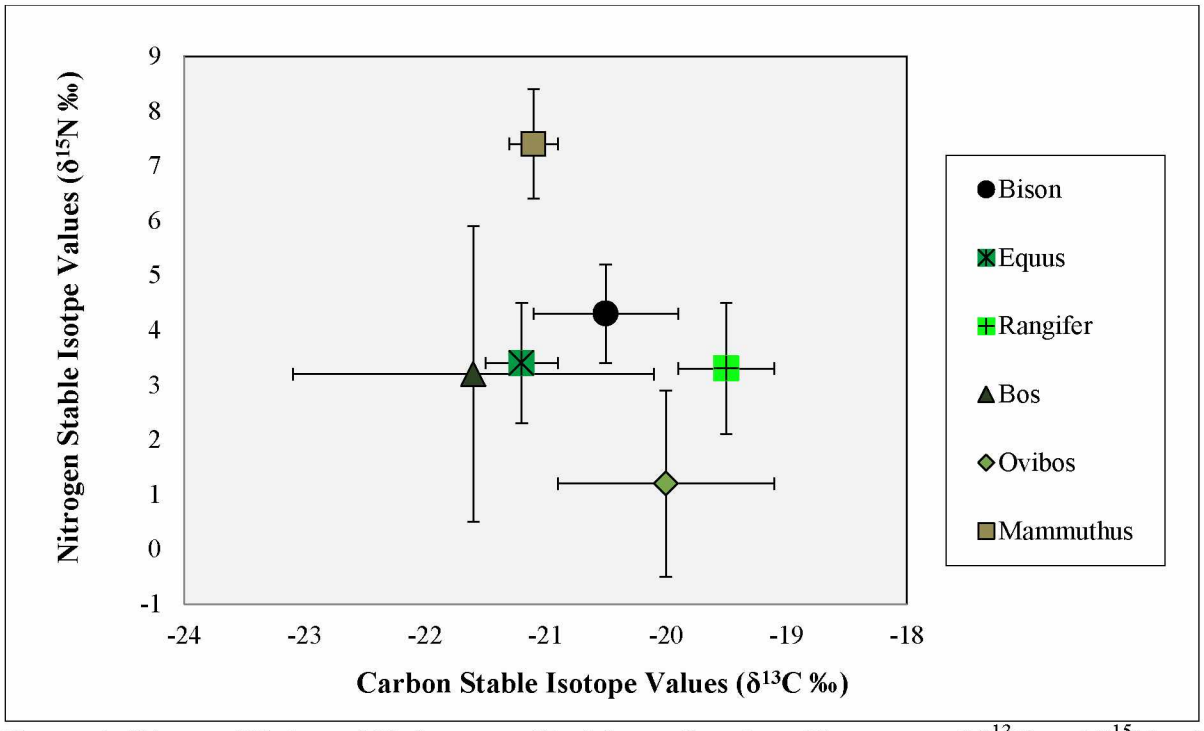

Figure 1. Dietary Niches of Pleistocene Herbivore Species. The range of $\delta^{13}C$ and $\delta^{15}N$ values are based on values published in Fox-Dobbs et al. 2008. The mean is derived from pre-glacial, full-glacial, and post-glacial values. Error bars represent standard deviation, but may be exaggerated due to averaging across temporal periods.

Equus. Similar to the results from Fox-Dobbs et al. (2008), this indicates that while there may have been a small degree of competition between some species for certain food sources, herbivores in general occupied separate dietary niches. Their results also showed that the largest change in isotope ratios for steppe bison occurred around 25,000 BP, with a sharp decrease in both $\delta^{13}C$ and $\delta^{15}N$ values (Mann et al. 2013). The cause of the shift is not known, but coincides with the Last Glacial Maximum; Mann et al. (2013) suggest this indicates that the shift was caused by global climate change and not changes in bison foraging behavior. However, comparing the results of this study (Mann et al. 2013) with the Fox-Dobbs et al. (2008) study suggests that there may have been different patterns of niche partitioning, and that herbivore habitat and forage likely varied across the Pleistocene landscape.

Steppe bison mobility patterns and diet choice were also reconstructed for a cohort of European *Bison priscus* by Julien et al. (2012) using isotopic methods similar to those employed in this thesis. The specimens were excavated from the site of Amvrosievka in Ukraine dated to the LGM. The results showed that the bison population was non-migratory during the LGM and likely stayed in a relatively contained habitat throughout the year. Additionally, a slight increase in $\delta^{13}C$ values during the winter suggested that the bison were consuming lichens when other forage was unavailable. Julien et al. (2012) suggested that this pattern of consumption indicated that the herd did not need to move on a seasonal basis, but instead adapted their diets to the seasonally available forage. The authors further argued that steppe bison were a large component of prehistoric subsistence economies in that region during the Late Pleistocene because bison would have represented a predictable and plentiful resource throughout the year, and were relatively immobile (Julien et al. 2012).

Collectively, the information derived from previous characterizations of steppe bison behavioral ecology provides several expectations for how populations in Alaska may have behaved. Based on sexual dimorphism, modern herd behavior, and isotope analyses, steppe bison may have occupied large habitat ranges but likely were not seasonally migratory (e.g., Guthrie 1990; Julien et al. 2012), or perhaps, were not seasonally migratory in certain ecological regions or during certain time periods (e.g., the LGM). Steppe bison also appear to have occupied a variety of habitats and consumed a far wider range of vegetation than modern bison do (e.g., Rivals et al. 2007), and their diets may have more closely reflected the diets of wood bison. However, unlike some ungulates which shifted their diets during the Pleistocene-Holocene transition, bison appear to have continued consuming the same types of forage as they did during previous climatic periods, and this may have been what lead to their eventual decline

(e.g., Rivals et al. 2010). Dietary reconstructions also demonstrate that bison occupied slightly different dietary niches than other grazing species and that they experienced a large shift in isotope values around 25,000 BP (e.g., Fox-Dobbs et al. 2008; Mann et al. 2013).

2.3 Paleoenvironmental Context: Changes Over the Past 50,000 Years

The vegetation and climate of interior Alaska has changed many times over the past 50,000 years. Understanding what the past environment was like is important for studies seeking to address the behavioral ecology of any paleo-species. Research on modern bison herds has demonstrated that bison behavior is constrained by the surrounding environment (*c.f.,* Gates et al. 2010; Meagher 1986; Plumb et al. 2014), and can vary based on a number of factors including the physical landscape, forage availability, seasonality, precipitation, population density, and predation. The bison specimens in this study encompass a wide temporal span, dating from earlier than 40,000 to ~17,000 BP. Because of this, a brief overview of the climate, vegetation, and habitat changes that occurred over the past 50,000 years in Alaska is presented, and helps to contextualize the results of this study.

This study encompasses two geologic epochs: the Pleistocene, which was a worldwide cool and dry glacial period, and the Holocene, which is the current interglacial period and is characterized by a warmer and wetter climate. During the Pleistocene, sea levels were much lower and Alaska was part of a larger landmass that stretched from northern Europe through Siberia and into northern Canada. The areas that were above sea level and adjacent to the Bering Strait, including Alaska, the Yukon Territory, and western Siberia, are referred to as *Beringia* (see Figure 2; Hopkins 1967). Pleistocene environments have been the subject of a great deal of research, beginning in the late 19th century when the skeletons of extinct megafauna such as

woolly mammoth, bison, and saber-toothed cats were uncovered as part of exploration and mining activities (*c.f.,* Hopkins 1982). While the Pleistocene and Holocene were worldwide climatic periods, there were also smaller-scale, regionalized fluctuations in climate and precipitation throughout the two periods. These fluctuations would have altered the forage and habitat availability for large bodied herbivore species like bison, which, in turn, would have likely impacted the behavioral ecology and stability of those species.

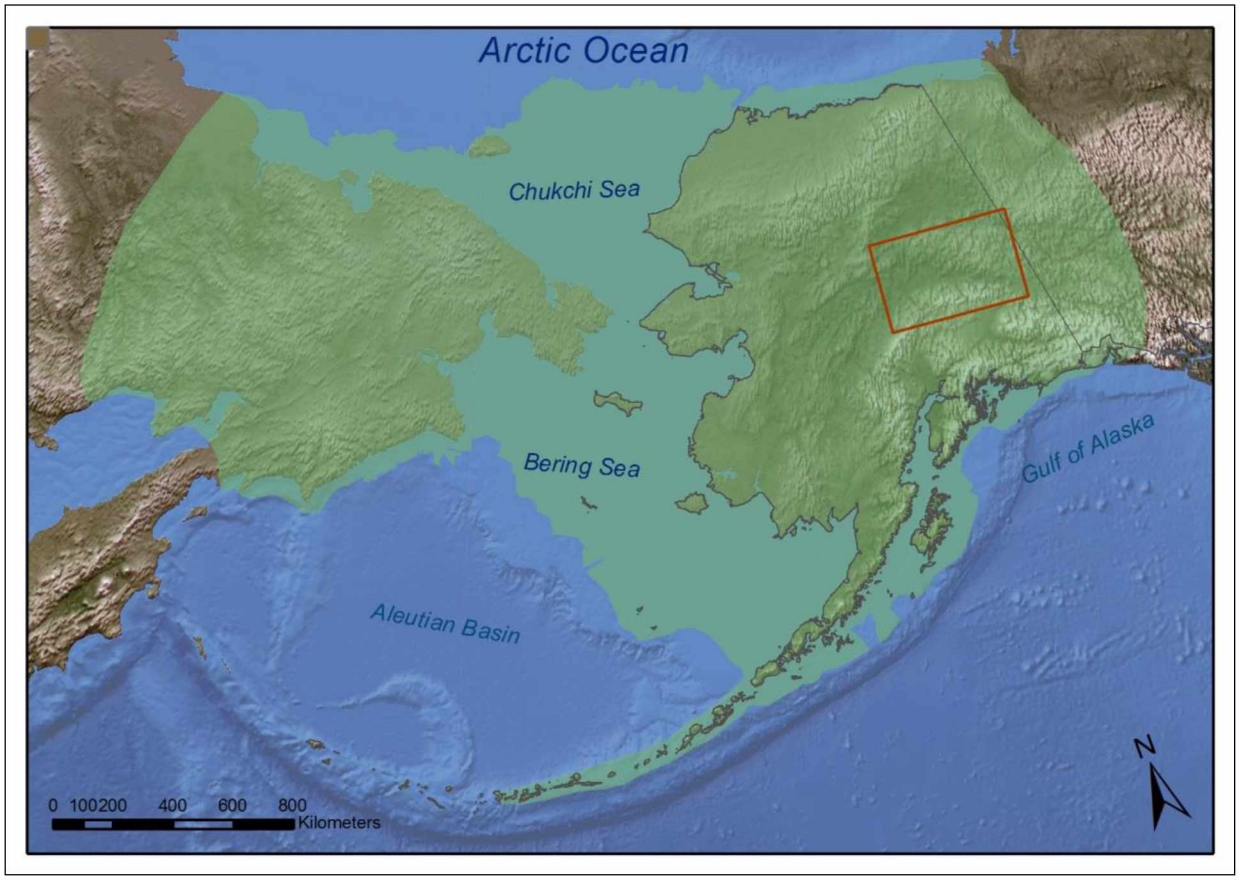

Figure 2. Map of Beringia during the Pleistocene. The region that is shaded green represents the above sea level during glacial periods; the orange reference box bounds the Tanana Basin and YTU.

Pleistocene environments in Beringia seem to have been much more dynamic than at present. Glaciation in mountainous areas contributed to the shifting landscape by forming large outwash plains as they expanded and retreated; additionally, extensive dune fields were created from sand that was constantly transported by wind, especially in river valleys (Péwé and Reger 1983; Thorson 1990). Large soil particles from Pleistocene stratigraphic deposits suggests that winds were incredibly strong, causing soil to be continually eroded from one place and deposited elsewhere (Begét 2001), which would have created thick clouds of dust that swept across the dry northern steppes. Guthrie (1990, 2001) noted that these strong dust storms would have mixed with snowfall during the winter, and when spring came, the dark snow likely would have melted incredibly fast, creating torrents of water that would have rushed downslope, creating mudslides and burying anything in its path. Additional evidence of this rapid spring break-up can be found in the large number of faunal deposits that can only be the product of rapid downslope alluvial transport or mass movement of seasonal thaw deposits by solifluction (Guthrie 1990; Thorson and Guthrie 1992).

Weather patterns during the Pleistocene were also very different because such of a large volume of atmospheric water, responsible for the weather patterns and oceanic storm currents experienced today, was locked away in the form of glaciers. The Bering Land Bridge itself would have also altered weather patterns as it cut off circulation between the North Pacific and Arctic Oceans (Hu et al. 2010). Beringia likely also experienced hyper-continentality, as physical features such as the Himalayas would have affected the climate by creating a monsoon shadow that blocked precipitation from Southeast Asia from reaching northern regions of the globe (Guthrie 2001). Large terrestrial ice sheets in Scandinavia and Eurasia would have also created widespread aridity for circumpolar regions (Siegert et al. 2001). Based on the presence

of short-legged animals such as the saiga antelope (*Saiga tatarica*), snowfall was also likely much lower during the Pleistocene, which would not have been able to survive in deep snow, and this would have contributed to the already dry climate (Guthrie 1982b). Snow that did fall likely did not remain on the ground for long, but instead was carried away by strong katabatic winds that swept off of glaciated areas; this would have also caused dust and snow to mix together, decreasing albedo and expediting spring breakup (Guthrie 1990, 2001).

2.3.1 Pleistocene Vegetation Communities

The Pleistocene faunal species that inhabited Beringia comprised a diverse biota that is not paralleled in any modern settings today. There have been many questions about how the vegetation, typically not associated with a carrying capacity for such a large biomass, could support the diversity of creatures which roamed the landscape. This has been termed the 'productivity paradox' (i.e., Guthrie 1990, 2001; Yurtsev 2001) and has been the focus of many paleoecological reconstructions. Whatever the vegetation regime of Beringia, there are no exact modern analogs today, which make vegetation reconstructions challenging (Elias 2001).

Grazing lawns were one possible mechanism that supported the high biodiversity of megafaunal species (Guthrie 1982b, 1990, 2001; Zimov et al. 1995). Research on modern grazing herbivores has demonstrated that they help maintain a high plant biodiversity, and that the absence of large grazers in an ecosystem can have dramatic impacts on local vegetation and other species (e.g., McNaughton 1984). Grazed areas can have over twice as much biomass for grasses and leaves, resulting in a higher diversity of grazing species in those areas (McNaughton 1984). Because of this, gregarious grazers such as bison can change the vegetation structure and increase foraging efficiency of an area, which in turn, increases habitat productivity and

availability for other species. If large grazers such as mammoth and bison (possibly representing as much as 75% of the Beringian biomass; Mann et al. 2013), began to decline, it would have dramatically affected the availability of plant resources for other grazing species, and could have contributed to a top-down collapse of the steppe ecosystem during the end of the Pleistocene, similar to the model Zimov et al. (1995) proposed.

Early reconstructions of past vegetation in Beringia suggested that the steppe ecosystem as a homogenous wasteland of grass, stretching for thousands of miles with little to no change in the distribution or abundance of plant species (Hopkins 1982); however, this view has changed. Schweger (2008) summarized recent vegetation reconstructions for Beringia and noted that descriptions of the kinds of plant communities that were present in the past are often contradictory, ranging in characterization from modern tundra (Anderson et al. 1989; Colinvaux 1967), to mesic-adapted shrub-tundra (Elias et al. 1996), to predominantly xeric steppe-grasslands interspersed with some shrub-tundra (Guthrie 1990; Zazula et al. 2006). However, Schweger (2008) suggested that this range in characterization is due to the fact that many of the studies have focused on limited vegetation ranges, when in reality, the landscape was likely not homogenous, but characterized by many different localized ecotones representing different vegetation patches and micro-environments that also changed through time.

Evidence for vegetation patchiness during the Pleistocene is indicated from a variety of sources like pollen data (Ager 2003; Bigelow and Powers 2001; Bigelow et al. 2003), stable isotope analyses of plant material (Wooller et al. 2007), food web reconstructions (Fox-Dobbs et al. 2008; Mann et al. 2013), plant micro- and macrofossil identification (Wooller et al. 2007; Zazula et al. 2006), and insect remains (Elias 1992; Elias and Crocker 2008). Together, this research has demonstrated that vegetation communities throughout Beringia were composed of a

mosaic of different patches and localized environments. While the dominant vegetation was characterized by herbaceous perennials and graminoids like grasses, sedges, and forbs, there were also low percentages of shrubs, mosses, and lichens (*c.f.,* Schweger 2008). Trees were rare, but *Salix, Betula,* and other shrub species likely grew in low elevation drainages and other protected areas.

In general, the vegetation of western Beringia appears to have been more xeric-adapted, while eastern Beringia appears to have been more mesic-adapted (Anderson and Lozhkin 2001; Elias 1992; Elias and Crocker 2008; Guthrie 2001). The vegetation communities may have been arranged by altitudinal clines, aspect, proximity to water, or other factors, and would have composed a mosaic of different ecozones. While this diversity in vegetation communities would have allowed for different grazing niches for Pleistocene herbivores (*c.f.,* Fox-Dobbs et al. 2008), this factor may have created a barrier and prevented migration between eastern and western Beringia (*c.f.,* Elias and Crocker 2008; Guthrie 2001). Additionally, because the vegetation was parsed out into patches, climate-based shifts in the vegetation communities was probably not uniform across the landscape, and this could have contributed to the herbivore population instability at the close of the Pleistocene.

2.3.2 Last Interstadial (Marine Isotope Stage 3)

The last interstadial period (also known as the Middle Wisconsin/Karaginsky Interstadial) occurred during Marine Isotope Stage 3 (MIS3) between 57,000-29,000 BP and followed the period of maximum Pleistocene glaciation between 71,000-57,000 BP (Elias and Brigham-Grette 2013; Lisiecki and Raymo 2005). This period is not as well understood in Beringia as later climactic periods, but was characterized by a general warming trend that allowed for an

expansion of trees and shrubs, and was likely similar to Early Holocene environments. In western Beringia, forests nearly reached modern distribution, while in eastern Beringia, forests expanded but remained limited to valley bottoms and low elevation areas (Anderson and Lozhkin 2001). In Alaska, the interstadial period peaked around 35,000-33,000 BP, and during this time trees and shrubs reached their maximum distribution (Anderson and Lozhkin 2001). Prior to this interstadial peak, conditions seem to have been more xeric, with a predominance of herbaceous shrub-tundra with the presence of some *Betula* and *Alnus* shrubs between 43,000-38,000 BP (Anderson and Lozhkin 2001). Reconstructions of sedimentation rates at the CRREL Permafrost Tunnel near Fairbanks indicate a dry climate with sparse vegetation, and permafrost seems to have expanded during this period, indicating that while the climate had ameliorated from previous periods, it was still relatively cool and dry (Hamilton et al. 1988)

In many ways, the Early Holocene is a good model for climate and vegetation during the latter half of MIS3. During this time, "macrofossil and pollen data imply a moister environment than previously, and one that may be somewhat analogous to that found in modern systems" (Anderson and Lozhkin 2001:113). Dated plant macrofossils from interior Alaska indicate that by 35,000 BP, *Picea, Betula, Populus*, and *Larix* had almost reached modern distribution, but were not as densely distributed as today (Hopkins et al. 1981). Begét (1990) also found evidence of decreased sediment accumulation between 32,000-30,000 BP, which suggests a period of increased warmth and spread of vegetated surfaces which prevented erosion and deposition in Alaska. On a more local scale, analysis of soil core pollen from the Isabella Basin near Fairbanks indicates that between 34,000-30,000 BP, the vegetation in the region was predominantly open sedge with some *Picea* forests in favorable locations, along with shrub *Alnus, Betula*, and *Larix* occurring in some areas (Matthews 1974). Wooller et al. (2007) also

reconstructed vegetation regimes near the CRREL tunnel through isotopic analysis of plant remains, and found that $\delta^{13}C$ values indicated relatively wet habitats, similar to modern environmental conditions.

2.3.3 Last Glacial Maximum (Marine Isotope Stage 2)

The Last Glacial Maximum (also known as the Late Wisconsin/Sartan Glaciation) occurred at the end of the Pleistocene during Marine Isotope Stage 2 (MIS2) between 29,000-14,000 BP (Elias and Brigham-Grette 2013; Lisiecki and Raymo 2005). MIS2 was a stadial period and glaciation significantly advanced in many regions of the globe. In Alaska, approximately 750,000 km^2 of high elevation and mountainous areas were covered in glaciers at the height of the LGM (Kaufman and Manley 2004). However, the extent of glaciation during MIS2 was much less than during maximum glacial expansion (i.e., Early Wisconsin Glaciation) which occurred during Marine Isotope Stage 4 (MIS4) between 71,000-57,000 BP (Lisiecki and Raymo 2005). The glaciation during MIS4 covered over a million square miles in Alaska (Kaufman and Manley 2004). Even though much of the Brooks and Alaska Ranges were glaciated during the Pleistocene, most of interior Alaska remained unglaciated during both MIS4 and MIS2, including the Tanana and Yukon River basins (Kaufman et al. 2011). Portions of the YTU were glaciated during MIS4, but the glaciers retreated and were only present in small patches at high elevation during MIS2 (see Figure 3; Kaufman et al. 2011).

The climate during MIS2 was considerably cooler than previous periods, and much of the atmospheric water was removed from global weather patterns in the form of glaciers, creating a much more arid climate as well (Hopkins 1982). Schneider von Deimling et al. (2006) estimated that during the LGM, mean annual temperatures would have been between 4.3-9.8°C colder than

at present, and this would have been enough to significantly alter weather and vegetation patterns. On a more local level, Viau et al. (2008) estimated that mean July temperature in Eastern Beringia would have been 4°C colder than present, and Elias (2001) estimated that temperatures in the Yukon were as much as 7.5°C cooler around 22,000 BP. However, this decrease in temperature was not uniform across Beringia or uniform seasonally; Kurek et al. (2009a) estimated that mean July temperatures in Western Beringia were not decreased during MIS2, and actually echoed modern values. This indicates that there were east-to-west trends in temperature and moisture variation, with colder and drier conditions centered over eastern Beringia (Elias and Brigham-Grette 2013).

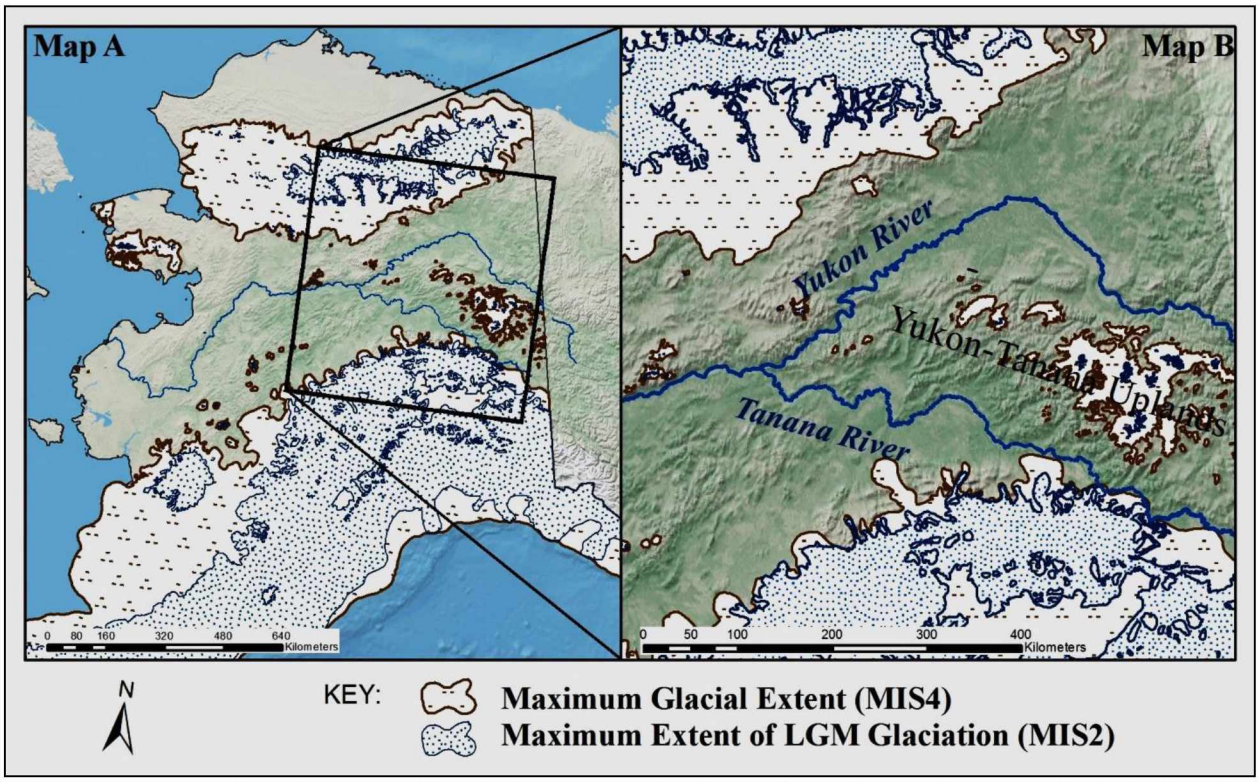

Figure 3. Map of Pleistocene Glaciation. Map A shows the estimated extent of glaciation for all of Alaska; Map B is zoomed into the Yukon Basin, YTU, and Tanana Valley. Glacial extents derived from Alaska PaleoGlacier Atlas (Version 2) dataset (Kaufman et al. 2011).

The vegetation during the LGM was dominated by graminoids; however, there was likely a much greater diversity of herbaceous vegetation than previously thought (e.g., Yurtsev 2001). The presence of *Populus, Picea, Pinus, Betula* and *Alnus* pollen throughout Beringia during the LGM, suggested these species remained in restricted areas even during the harshest periods (Brubaker et al. 2005). Yurtsev (2001) characterized the vegetation during the LGM into 3 main categories, including 1) watersheds and hills slopes which had cold-adapted herbaceous shrub vegetation, 2) valleys and lowlands areas with xeric-to-brackish steppe-meadows, and 3) in the lowest elevation regions of the Bering Land Bridge shrub tundra dominated and served as a barrier to flora and fauna on either side. Elias (1992) was the first to note the presence of this barrier, and referred to it as a mesic belt which acted as "some kind of biological filter that blocked the movements of some steppe-tundra plants and animals across the Bering Land Bridge" (Elias and Crocker 2008:2482).

2.3.4 Pleistocene-Holocene Transition

At the close of the Pleistocene, the climate in Beringia and other regions of the world dramatically shifted. During this period "virtually every component of the climate system underwent large-scale change, sometimes at extraordinary rates"; this was triggered by seasonal insolation anomalies, increased CO_2 emissions, rapid sea-level changes, and freshwater influxes into ocean currents (Clark et al. 2012:11340). Two world-wide climatic events known as the Bølling-Allerød and Younger Dryas indicate that past climate did not simply get steadily warmer, but that there were fluctuations in the general warming trend as well (Cronin 1999). To already unstable plant and animal communities, these fluctuations would have been stressful and likely played a large role in population declines and extinctions for many of the megafaunal

species (*c.f.,* Lorenzen et al. 2011).

The Bølling-Allerød was a general warming trend that has been identified around circumpolar and temperate regions of the globe between 15,000 and 13,000 BP (Cronin 1999). In general, this period was warmer and wetter than previous glacial times, but the vegetation was still similar to Pleistocene flora. Pollen samples from interior Alaskan lake cores indicate an increase in birch and willow, with presence of alder, sedges, and grasses as well, suggesting an increase in mesic-adapted shrub-tundra biome during this period (Bigelow and Powers 2001). As plant communities began adapting to the warmer and wetter conditions, this would have caused a shift in the availability of grasses and sedges for grazing herbivores. Milankovitch cycles during this time would have added to this factor by increasing the disparity between seasons, and causing temperature difference between summer and winter to be more extreme than at present (Guthrie 2001).

In contrast to the warm Bølling-Allerød, the Younger Dryas was a period of cooling between 12,800 and 11,500 BP (Rasmussen et al. 2006; Hua et al. 2009; Kokorowski et al. 2008). This cooling trend may not have been uniformly distributed throughout Beringia; however, and there is limited evidence for severe environmental and ecological changes during the Younger Dryas in northern Alaska (Kokorowski et al. 2008) and the Yukon (Kurek et al. 2009b). Glaciers appear to have expanded and advanced, at least in the higher elevation areas of the Alaska Range (Briner and Kaufman 2008; Young et al. 2009), suggesting that temperatures were cooler during this period. Similar to previous Pleistocene landscapes, the depositional environment was still very active, with sand and loess being deposited by intense winds that prevented soil formation (Bigelow et al. 1990; Dilley 1998; Reuther 2013). Vegetation reconstructions from interior Alaska suggest that the Younger Dryas was a return to a more

Pleistocene-like climate and environment with decreased precipitation and temperature and re-expansion of herbaceous-shrub vegetation, although vegetation was likely variable across ecotones (Bigelow and Edwards 2001; Bigelow and Powers 2001).

2.4 Summary

Even though there are no extant herds of bison in Alaska today, an abundance of paleontological, archaeological, and ethnographic data indicates that they were important components of the ecosystem throughout the Pleistocene and important subsistence resources for most of human prehistory. The history of bison in Alaska is enigmatic; even though they weathered the dramatic climate changes during the Pleistocene-Holocene transition, bison eventually became extinct in Alaska, likely within living memory (Stephenson et al. 2001).

An overview of the changes in vegetation, habitat, and climate provides context for understanding how bison behavior may have changed in response to the environment. As summarized, there were many environmental changes throughout the past 50,000 years which likely constrained bison behavior and population stability. Based on genetic reconstructions, steppe bison populations seemed to have been the most unstable during warmer and wetter periods, which may explain their eventual extinction during the Holocene. While this chapter has provided the background and environmental context for bison in Alaska, reconstructing the behavioral ecology of an extinct species and contextualizing it with regards to human foraging decisions requires the use of several theoretical perspectives. These perspectives are discussed in the next chapter and are based on the Principle of Actualism and HBE.

CHAPTER 3: THEORETICAL APPROACHES

Two primary theoretical perspectives are used in this study. The first perspective is the Principle of Actualism, which provides the foundation for reconstructing bison behavior ecology from modern proxy data and isotopic analysis of skeletal remains. The Principle of Actualism assumes that biologic organisms behaved the same in the past as they do today. This theoretical perspective is frequently used to reconstruct the behavioral patterns of past species but can be problematic as animal behavior is often influenced by environmental factors (*c.f.,* Johnson et al. 2001; Plumb et al. 2014). Because of this, behavioral reconstructions for past species should incorporate both modern analogs and direct biomolecular analysis of skeletal remains. This study applies both methods, and a summary of modern bison behavior is provided in this chapter and is used to contextualize the biomolecular results (discussed in Chapter 7).

The second theoretical perspective is Human Behavioral Ecology (HBE), which provides expectations about behavior, as well as models of subsistence and settlement strategies, for foraging societies. A summary of the interior Alaskan archaeological record is also presented, especially focusing on the subsistence and settlement patterns during the Late Pleistocene and Early Holocene in the Tanana Basin. This information, combined with perspectives from HBE, presents several expectations for how human behavior could have been structured by bison mobility patterns in the past.

3.1 The Principle of Actualism: Inferences for Reconstructing Bison Behavior

Few archaeologists would deny that it would have been essential for prehistoric peoples to understand the behavior of key prey species, and indeed, there is a call for more studies that reconstruct the behavioral ecology of large game resources (i.e., Britton 2009; Frison 2004;

Graves 2010; Julien et al. 2012; Rivals et al. 2007; Widga 2006). Prey behavior likely influenced many human decision-making processes, and to be able to more fully understand this relationship, it is necessary for archaeologists to reconstruct the behavioral ecology of those species. This can inform on aspects such as human subsistence strategies, seasonal mobility, site location and function, land-use, and risk management. The Principle of Actualism (or simply actualistic studies) provides a theoretical framework for reconstructing past behavior. Actualistic studies use both direct and indirect methods for behavioral reconstructions, and often use proxy datasets such as the paleo record or modern species behavior. However, this method is not without issues. One key problem is that many species that were present in the past are now extinct, and because the environment can play a large role in shaping animal behavior, it can be difficult to find analogs for past environments and species. Because of these issues, analyses at the biomolecular level are becoming more prevalent, and have the ability to more accurately and thoroughly reconstruct past behavior.

The Principle of Actualism was first developed through early geologic inquiry (i.e., Charles Lyell), and borrowed heavily from the principle of Uniformitariansm (i.e., James Hutton; Cannon 1976). Actualism is the idea that natural processes that operated in the past operate the same way that they do today, and therefore those processes can be reconstructed through direct observation (Rutten 1957). This theoretical "leap of faith" prevails in all studies of the past (Yellen 1977:274), including geology, paleontology, archaeology, paleobiology, and paleoecology. Actualistic studies are frequently used in archaeology for zooarchaeological and taphonomic reconstructions (e.g., Gifford-Gonzalez 1991; Lyman 2004) and often rely on proxy datasets for behavioral and environmental reconstructions. Gifford-Gonzalez (1991) outlined several theoretical principles that guide actualistic studies, and key among those principles are

formal and relational analogies. Formal analogies are obtained through direct observations and include factors such as physical appearance and depositional environment, while relational analogies are obtained through inference and include factors such as behavior and ecology that can never be directly reconstructed.

Actualistic studies are frequently used in paleontology to reconstruct the behavioral ecology of prehistoric species, including factors such as population dynamics, feeding behavior, mobility, or other aspects. The methods used for the reconstructions typically include both direct and indirect methods (i.e., formal and relational analogies, *sensu* Gifford-Gonzalez [1991]). An example of both methods can be found in Guthrie's (1990) work on reconstructing the behavioral ecology of steppe bison. He reconstructed physical traits such as size, sexual dimorphism, and pelage characteristics through formal analogies on actual skeletal remains. However, he relied heavily on relational analogies for reconstructing other behavioral factors, including group size, social structure, mobility patterns, and other behavioral characteristics. These analogies were based on environmental constraints, modern bison behavior, and physical traits, information about which allowed him to infer the behavioral characteristics that were not direct observations (1990). Guthrie's reconstruction remains one of the best to date for steppe bison behavioral ecology during the Pleistocene. However, actualistic studies such as that one are problematic in that the inferences are never tested, and there is no way to know if the inferred behavior would have been reflective of actual steppe bison behavior.

Actualistic studies that have used relational analogies for reconstructing the behavioral ecology of past species have been criticized (*c.f.,* Britton 2009; Julien et al. 2012; Rivals et al. 2007). Britton (2009) noted that there are many issues with actualistic studies, including that for many species and environments, there are no modern analogs, and animal behavior is often

variable based on environmental influences. For example, woolly mammoth (*Mammuthus primigenious*) is an extinct proboscidean species that lived in northern latitudes during the Pleistocene. There are no modern analogs for cold-adapted proboscideans, or for the steppe-tundra vegetation and environment in which they lived; however, modern elephants are often used an analog for reconstructing woolly mammoth behavior (e.g., Haynes 1991).

Populations of the same species can also demonstrate variation in behavior based on environmental constraints. For example, caribou populations can be both migratory and non-migratory depending on food availability and social structure (Johnson et al. 2001). Modern bison behavior is clearly influenced by environmental factors and can vary based on forage availability, climate, seasonality, social structure, or other factors (Gates et al. 2010; Meagher 1986; Plumb et al. 2014). Behavioral changes can also occur on a historical scale. This has been documented in migration patterns for North American caribou (Mahoney and Schaefer 2002) and bison populations (Bamforth 1987; Cannon 2001) over the past two centuries (although these behavioral changes are likely influenced by anthropogenic factors). Due of the problematic nature of using modern species as proxies for animals in the past, it is often more realistic to reconstruct past behavior directly from skeletal remains. Modern analogs can provide some context to direct studies however. Modern bison herd behavior is summarized in the following subsection:

3.1.1 Modern Bison Behavior

Wood bison and plains bison are both directly descended from steppe bison (Shapiro et al. 2004; van Zyll de Jong 1993), which makes them the best-suited modern proxies for deriving expectations about steppe bison behavior. Like their steppe ancestors, modern bison have been

heralded as a key-stone species that is essential for maintaining ecosystem balance (Knapp et al. 1999) and have been described as "ecosystem engineers", creating and maintaining grassland and meadow ecosystems by grazing, stimulating nutrient cycling, dispersing seeds, and creating habitat for other species (Grogan et al. 2010:160). Modern bison behavior is relatively plastic, and can vary based on multiple environmental factors. However, there are some similarities shared by all North American bison populations, such as social behavior and dietary requirements. Additionally, specific behavioral responses to seasonality, landscape, forage availability, predation, snowfall, and other factors can provide some expectations about how bison in past may have responded to similar situations.

3.1.1.1 Seasonal Herd Structure

Bison display social gregariousness and form large herds. For most of the year females, calves, and juvenile males (less than three years of age) make up what are known as matriarchal herds, while adult males are typically solitary or form small bachelor bands of 2-3 individuals that are peripheral to the main herd (Meagher 1986; Olson 2005; Plumb et al. 2014). However, the social structure of bison herds is variable and depends on many factors including mating, age of individuals, forage availability, environmental productivity, and season. Typically, herds are larger in more open habitat and are smaller in closed habitats (Meagher 1986; Van Vuren 1983).

Both wood and plains bison display reproductive synchronicity, which means that they always give birth in the spring in predictable and constrained patterns (Berger and Cunningham 1994). Assumedly, steppe bison would have also followed this pattern, and birth synchronicity also appears to be more constrained in northern latitudes (Gates and Larter 1990), suggesting that steppe bison calves would have always been born during a short period in the spring. Calving

season lasts for about two months for modern bison, with and calves are born between May and June in northern latitudes; however, out-of-season births have been recorded for most herds (Meagher 1986; Plumb et al. 2014). During calving season the herd structure is the typical matriarchal band, but pregnant females often segregate themselves from the herd prior to calving and then rejoin the herd a few days after birth (Olson 2005).

Mating season is when the largest herds form, and includes both sexes of all age classes (Berger and Cunningham 1994; Lott 1981). Males join the matriarchal herds for the rut, which lasts from late June through September in lower latitudes (Plumb et al. 2014). In higher latitudes, breeding season starts about a month later, lasting from late July through September and peaking in mid-August (Fuller 1960; Meagher 1986). While the large aggregate breeding herd only lasts 6-8 weeks, the forage requirements for that number of animals forces them to constantly be on the move in search of new grazing areas. After the breeding season, the animals fracture into smaller groups again, thus enabling them to spend longer in vegetation patches and decrease their movements (Olson 2005).

Winter is the most difficult season for bison, especially at northern latitudes. Depending on temperature, snowfall, and predation, bison can either congregate into relatively large herds (a safety mechanism) or they can split into smaller groups of around a dozen individuals when there is a lack of forage (Plumb et al. 2014). Hess (2002) noted that free-ranging bison in Yellowstone have an average early winter herd size of ~250 individuals, but by spring the larger herds fracture into many smaller groups of about 15 individuals. Bison often seek protected areas in the winter such as river valleys and low elevation areas or regions with tree cover (Olson 2005). Other factors that seem to influence seasonal aggregation behavior include forage and environmental conditions, population size, and physical landscape (Plumb et al. 2014).

3.1.1.2 Dietary Requirements

Both wood and plains bison are very efficient foragers and use a variety of habitats based on forage availability (Plumb et al. 2014). They are predominantly grazers, but do incorporate a small amount of browse into their diet when grazing sources are scarce (Larter and Gates 1991). Bison have a four-chambered stomach which allows them to digest fibrous forage and their preferred diet is graminoids (grasses and sedges) but supplement their diet with herbaceous forbs and occasionally woody vegetation (Larter and Gates 1991). However, bison diet is variable depending on the abundance and availability of plant species in their habitat range. Grasses and sedges compose about 90% of the diet for bison living on the Great Plains (Grogan et al. 2010). In mountainous regions or northern habitats, sedges can comprise more than 40% of bison diet (Grogan et al. 2010; Meagher 1986). European bison (*B. bonasus*), a distant cousin to North American bison, have been observed consuming up to 33% of browse during the summer (Boroski and Kossak 1972). The transplanted herds of plains bison in Alaska seem to favor parkland meadows or riverine and lacustrine environments and graze on grasses, sedges, and forbs, especially favoring vetch (*Vicia*), silverberry (*Elaeagnus*), willow (*Salix*), and dwarf birch (*Betula nana*; Alaska Department of Fish & Game 2015).

Wood bison inhabit a more varied environment than plains bison, and change their diet seasonally depending on forage availability and abundance. Wood bison typically graze on lowland meadow or forest vegetation during the winter, and then consume a more diverse variety of grasses, sedges, riparian vegetation, and shrubs during the summer months (Plumb et al. 2014). This pattern has been documented for a herd of wood bison in the Northwest Territories (Larter and Gates 1991). During spring the herd prefers mesic meadows and consumes sedges, grasses and shrubs. In summer they seek out willow savannahs, which have the largest

abundance of crude protein. As forage quality declines in the fall and winter, the bison begin using a wider variety of habitats and begin consuming larger quantities of lichens (Later and Gates 1991). However, Reynolds et al. (1978) documented a slightly different dietary pattern in the Slave River wood bison herd. The diet for the Slave River herd contained 29 different plant categories, but slough sedge and reedgrass represented the most common forage for all seasons, comprising over 75% of the winter forage and over 90% of the summer forage. Starting in late fall and continuing through midwinter, the bison would follow creek bottoms and sloughs and use small meadows for grazing. Reynolds et al. (1978) noted that in these areas the sedges often froze before curing, and therefore had a higher nutrient composition which is why the bison sought out these forage patches. Meagher (1973) also observed that plains bison living in mountainous habitats will follow similar diet and habitat patterns as wood bison, and have more diverse diets than do plains bison living low elevation regions.

3.1.1.3 Migration and Mobility Patterns

The migratory behavior and foraging habits of wood and plains bison vary. There are several factors that influence the timing and magnitude of seasonal migrations including the availability of forage, weather conditions, population density, learned behaviors, and interactions with other ungulates and predators (Plumb et al. 2014). Most free-ranging bison are seasonally migratory to some degree, with average movements of ~150 km/year in mountainous habitat and ~240 km/year in boreal habitat (Geremia et al. 2011; Meagher 1973, 1986; McHugh 1958; Soper 1941).

Traditionally, plains bison have been assumed to be seasonally migratory. Historical accounts described vast herds moving hundreds of miles north-to-south between summer and

winter ranges, while some herds remained on northern prairies throughout the year (Grogan et al. 2010). Additionally, herds in the Rocky Mountains were described as moving east-to-west seasonally, from mountain foothills in the summer to prairies in the winter (Grogan et al. 2010). However, this seasonal long distance migration migratory behavior may not have always characterized plains bison behavior, and there is evidence that bison may have migrated very little in the past (Epp and Dyck 2002; Graves 2010; Rivals et al. 2007; Widga 2006). Currently, bison herds in Yellowstone National Park spend summers at high elevation, and then move to lower elevation in the winter along rivers and valleys (Geremia et al. 2011; Meagher 1973). This pattern has also been observed in the transplanted plains bison herd near Delta Junction, Alaska, where the animals spend the summer in higher elevation plateaus, and winters in lower elevation areas along river confluences (D. Bruning, personal communication 2014). However, wood bison typically do not have predictable migration patterns, but instead have a large foraging radius through which they move during the year (Larter and Gates 1994).

For both plains and wood bison, range size and movement patterns are related to many factors, including forage and water availability, weather patterns, insects, snow depth, and seasonal behavior like mating calving and migrations (Plumb et al. 2014). Larter and Gates (1994) monitored the patterns of the Mackenzie Bison Sanctuary herd (*B. b. athabascae*) in the Northwest Territories and found that age, sex, and the availability of food are all factors that affect foraging patterns. Females and juvenile males had larger home ranges, which may be the result of consuming less nutritious forage which necessitates greater mobility; females and juvenile males averaged a median range of 1,100 km^2 over the course of a year, while adult males had smaller home range, averaging 200-400 km^2 (Larter and Gates 1994). Larter and Gates (1991) also monitored herds in the Wood Bison National Park in Alberta and found that

the animals traveled up to 50 km throughout the entire year, with a range size of 180-1440km^2. Van Vuren (1983) monitored mobility patterns of the Henry Mountain bison herd (*B. b. bison*) in southern Utah, which live in a low productivity and forested parkland environment. The Henry Mountain herd had an average summer range size of ~52 km^2, which he noted is larger than the foraging range for most grazing species, and also demonstrated that vegetation density plays a role in foraging radii and time spent in habitat patches (Van Vuren 1983). Van Vuren (1979) also found that in shrub-steppe habitat (i.e., similar to what steppe bison inhabited), plains bison often foraged at higher elevation, migrated further from water, and grazed steeper slopes than would be expected in other habitats. Houston (1982) found that in mountainous regions during the winter, plains bison spent an average of 1.9 days in a given habitat patch, and they preferred highly productive mesic meadows. Additionally, bison habitat ranges seem to increase with increased bison population density and in areas with limited forage or poor quality habitat (Gates and Broburg 2011). Population substructure can also influence mobility patterns, with segments of a population utilizing different portions of the landscape at different times (Joly and Messier 2001; Olexa and Grogan 2007).

This data on modern bison herd social structure, seasonal behavior, and dietary requirements provide important expectations for reconstructing steppe bison behavioral ecology. Modern bison behavior has been shown to vary based on environmental factors like changes in habitat and forage availability, precipitation, and elevation, and this information can provide expectations about how steppe bison behavior may have been similarly constrained in the past. Because steppe bison were an important subsistence resource for humans, those same responces to environmental variables could also have affected human landuse patterns. The following section discusses the archaeological record for interior Alaska, was well as expectations for how

humans may have utilized bison as a key subsistence resource, and how human behavior may have changed as bison behavior changed.

3.2 Putting People in the Picture: Identifying and Modeling Human Behavior

Alaska has been inhabited for over 14,000 years and modern Native peoples have a rich and varied cultural history that is reflected in the archaeological record throughout the state. The earliest sites are located in the Tanana River Valley (e.g., Potter et al. 2013b); however, there are thousands of sites scattered across Alaska that are indicative of complex and varied subsistence economies, landuse patterns, technological adaptations, and lifeways that represent all periods of human prehistory. For decades archaeological research in Alaska was dominated by a cultural history approach which focused on developing cultural chronologies based on stylistic similarities in formal tools; more wholistic interpretations of human behavior were largely ignored. Recently, a greater emphasis has been placed on more complete syntheses of the record, with research on regional landuse patterns, subsistence economies, settlement structure, and spatial patterning which has supplemented the lithic-heavy focus (i.e., Holmes 2001, 2008; Mason and Bigelow 2008; Mason et al. 2001; Potter 2005, 2007, 2008a-c, 2011, Potter et al. 2013a-b; Yesner 2001; Yesner et al. 2011).

3.2.1 Regional Archaeology of the Tanana Valley

The Tanana Valley has some of the oldest known archaeological sites in the Americas. The earliest known occupation of eastern Beringia has been identified at the site of Swan Point and dates to ~14,000 BP (Holmes 2011). The technology and subsistence at Swan Point closely resembles that of the Diuktai Culture (dating to between 20,000-13,000 BP) from the Yenisei

and Lena River basins in Siberia (Holmes 2011; Goebel 2002). It is thought that climate amelioration after the LGM was one of the main factors that allowed humans to migrate from central-Siberia into the Americas during the end of the Pleistocene (*c.f.,* Goebel and Buvit 2011). Soon after Swan Point was occupied, people seem to have quickly spread throughout Alaska, and there are numerous sites dating to between 13,500-11,500 BP in the Tanana Valley and other regions of Alaska and the Yukon (Bever 2006; Mason et al. 2001; Potter 2008a; Potter et al. 2013b). From a technological standpoint, these earliest sites have a wide range of lithic forms compared to later periods (Potter 2011) and this includes Diuktai-like microblade forms at Swan Point (Holmes 2011), triangular "Chidandn" points at Healy Lake (Cook 1969) and the Nenana River Valley (Powers and Hoffecker 1989), and many other forms of bifaces, scrapers, and projectile technology. The reasons for this wide-range of technology is not entirely understood, but some have proposed that it represented different colonization strategies for previously unexplored regions (i.e., Yesner 2001), specialization to specific subsistence economies (i.e., Potter 2008c, 2011), or even different cultural groups sharing and using the same landscape in similar ways (e.g., Hoffecker 2005).

Due to high rates of sediment accumulation, faunal preservation for Pleistocene-aged sites in the Tanana Valley is exceptional (compared to other regions in Alaska) and has allowed early diet and subsistence economies to be reconstructed from the faunal record. During this period the subsistence base appears to have been relatively broad-spectrum and included small game, waterfowl, and possibly fish (Potter et al. 2014; Yesner 2001); however, bison and wapiti were clearly key components, and their remains dominate faunal assemblages until at least 9,000 BP (Potter et al. 2013b). Around 10,000 BP, the Bering Land Bridge became submerged and cut off Siberia from the New World. From this point to ~6,000 BP, subsistence and technology

seems to have been relatively uniform throughout Alaska, with wedge-shaped microblade cores and lansolate-form bifacial technology representing the two primary technological systems, and broad-spectrum foraging, with an emphasis on bison and wapiti, representing the primary subsistence components (Potter 2008b).

Around 6,000 BP there seems to be a shift in bifacial technology and subsistence behavior, and this has been termed the Northern Archaic Tradition (Dixon 1985; Esdale 2008). The technology during this period is typified by notched-base projectile points, end scrapers, choppers, and notched pebbles (Dixon 1985). Microblade technology continues through this period, although microblades are absent in many components (Potter 2008a). There is also evidence for a shift towards a more caribou-dominated subsistence economy during this period, and settlement patterns were likely organized around the seasonal availability of resources (Holmes 2008; Potter 2008a). The Northern Archaic Tradition occurs coincidentally with the spread of boreal forest (Anderson 1984), but the relationship between the change in lithic form and environment during this period remains largely unexplored (Esdale 2008; Mason and Bigelow 2008). In general, research on Middle Holocene sites has been limited for the region compared to both pre and post-Middle Holocene periods, and the Northern Archaic Tradition represents somewhat of a void for Alaskan archaeology (*c.f.,* Esdale 2008; Potter 2008b; Rasic and Slobodina 2008).

Based on the archaeological record, the Northern Archaic Tradition seems to have lasted in interior Alaska for several thousand years. However, around ~1,500 BP there was an abrupt shift in technology and subsistence patterns which is known as the Athabascan Tradition (Dixon 1985). Bow and arrow technology was introduced around this time (*c.f.,* Hare et al. 2004), and the archaeological record indicates that there was a sharp decrease in lithic technology, but at the

same time, there was an increase in organic implements as well as the first presence of copper artifacts (Dixon 1985). Faunal remains from this period suggest that salmon fishing dominated as the primary subsistence activity in the summer, although caribou and small game also contributed to the diet. Additionally, site occupations appear to have been longer and more substantial, site location and landuse patterns and were structured around the seasonal availability of resources (Potter 2008b; Shinkwin et al. 1980).

Potter (2008b) has suggested that behavioral changes during the Athabaskan period were driven by variation in the abundance and availability of prey species. Based on the archaeological record, it seems that around this time there was a crash in large-bodied ungulate species, which forced technology to be adapted to different subsistence resources and also caused shifts in settlement patterns towards a more sedentary lifestyle (Potter 2008b). There is clear continuity with this archaeological tradition and modern Athabascan peoples, with connections found throughout language and cultural practices (Holmes 1986; Kari 2005; Shinkwin et al. 1980), and the ethnographic record (e.g., McKennan 1959; O'Brien 2011).

The previous broad periods are generally accepted in Alaskan archaeology; however, more specific and localized cultural chronologies are often disagreed upon (e.g., Dixon 1985; Powers and Hoffecker 1989; West 1967). Most cultural chronologies for Alaska are based on a normative view of cultural history (i.e., Phillips and Willey 1953; Spaulding 1953) that was based on perceived differences in lithic form. From this perspective, regional tool typologies were developed for Alaska that were based on observed stylistic similarities in 'diagnostic' lithic forms, typically based on a few type sites with poor excavation and chronological control. Little effort was put into addressing the spatial distribution of sites, economies, seasonality, resource availability, excavation biases, functionality, or any other factors could influence assemblage

structure. Formal tools were thought to indicate culturally distinct populations, each expressing a singular form of lithic technology that represented normative behavior. While this approach has been criticized for decades as being a poor perspective for attempting to assign ethnic or cultural affinity (e.g., Binford 1962, 1965; Caldwell 1959), most of the cultural chronologies for Alaska are based on this approach.

One especially controversial topic in Alaskan archaeology is the perceived dichotomy between bifacial and microblade technology (Goebel et al. 1991; Goebel and Buvit 2011; Potter 2011; Powers and Hoffecker 1989; West 1967; Wygal 2011). One interpretation is that the technological systems represent distinct cultural groups that produced tools in a normative way based on cultural tradition (Dixon 1985; Goebel et al. 1991; Powers and Hoffecker 1989). The other interpretation focuses on function and suggests that lithic variability and patterning is the result of subsistence, landuse, or environment. Potter (2008a, 2008b, 2011) has demonstrated that bifacial technology has greater association with upland sites, while microblade technology is associated with lowland sites, suggesting that landuse and economy likely was a structuring factor for lithic variability.

Additionally, it has been argued that composite weapons systems with inset microblades may represent technology associated with bison hunting (Holmes and Bacon 1982; Guthrie 1990). Potter (2011) noted that bison faunal remains and microblades co-occur in 71% of site components dating to the Late Pleistocene and Early Holocene. Potter (2008a) has suggested that the higher proportion of microblade components in lowland settings is an indication that microblade technology was associated with bison hunting, while bifaces, likely part of an atlatl and dart system, would have been used for upland caribou and sheep hunting. This model is supported by emerging artifacts found in Alpine ice patches, which demonstrate that, at least for

the latter half of the Holocene, caribou were hunted with atlatls in high elevation and mountainous areas (Hare et al. 2004).

While this is only a brief summary of the archaeological record for the region, it does provide some key points that can help to contextualize the broader questions and themes in the region. This summary also demonstrates that exploring the human-bison relationship during the Late Pleistocene and Holocene can have implications for many aspects of interior Alaskan archaeology. This thesis further explores some theoretical perspectives from HBE, which has generated several expectations about how settlement and subsistence patterns may have been structured based on resource availability in the past.

3.2.2 HBE: Generating Expectations About Prehistoric Landuse Patterns

Human Behavioral Ecology is a broad theoretical framework that addresses behavioral adaptations in terms of fitness related trade-offs resulting from particular environments (Bird and O'Connell 2006). An advantage of HBE is that it uses strong heuristic models to explore human behavioral choices, and builds expectations for how that behavior would be reflected in the archaeological record. One of the main assumptions of HBE is that all human behavior seeks to maximize reproductive success. From this, other assumptions are generated which include 1) human behavior is adaptive, 2) humans behave optimally and seek to maximize their return, and 3) culture is an extrasomatic adaptive mechanism that allows humans to biologically adapt to a given environment (Binford 1962; Bird and O'Connell 2006; Kelly 2013; Winterhalder and Smith 1981, 2000).

This last assumption explicitly links *material culture* with *genetic inheritance*. The idea is that phenotypes, while biological, are structured by interactions of both biological and cultural

environments. However, HBE does not imply that behavior is actually controlled for by genes; rather, humans subconsciously evaluate which behaviors are optimal for reproductive fitness, and then those behaviors are selected for at the population level (Kelly 2013). In this light, cultural behavior is selected for and passed on from generation to generation, making it analogous to genetic inheritance (Kelly 2013). This analogy between biology and culture provides a strong framework for understanding human behavior in context of environmental constraints, including how the behavioral ecology of key prey species such as bison could have shaped decision-making processes in the past.

A main component of HBE is the use of models focused on the concept of diet choice, which seeks to determine the most optimal subsistence strategy under a given set of environmental conditions. These models have been collectively termed Optimal Foraging Theory (OFT) and are based on the assumption that fitness will be enhanced by maximizing the acquisition of food resources. These models seek to determine which food sources should ideally be consumed first and which should be ignored or would be insignificant components of the diet. When food sources that are considered "less optimal" are consumed, it is thought to indicate behavioral adaptations to less optimal environmental conditions (Smith 1983). While these models have been criticized as being inaccurate representations of actual human dietary behavior (Smith 1983), they are not intended to reconstruct actual diet choices, but rather generate expectations about certain conditions, and the optimal subsistence choices under those conditions. These models are not directly tested for in this study; however, they do provide expectations about human decision-making processes regarding diet choice and landscape use.

One of the first models to be developed was the *diet-breadth model* (MacArthur and Pianka 1966) that assumes the most productive food sources will be harvested and consumed

first. If those resources become scarce however, the cost of searching for them will increase and therefore will be replaced by other less-costly resources (Bird and O'Connell 2006; Kelly 2013). This model seems to fit the archaeological record of bison consumption during the Late Pleistocene and Early Holocene. There is evidence that bison, a meaty and predictable resource (i.e., high-ranking), were frequently harvested until the middle Holocene; however, there seems to have been a shift towards a caribou dominated economy shortly after this, indicating that the cost of searching for bison became too costly, and they were replaced with a lower-ranking resource. This dietary shift also may be a good indication of when steppe bison populations began to decline and became fragmented and unstable throughout Alaska.

Another version of this, the *patch choice model*, assumes that resources are grouped into patches on the landscape and the most productive patches will be selected for first (Charnov 1976; Kelly 2013; Smith 1983). The assumptions of this model imply that people would systematically seek out regions on the landscape where bison were located and would stay in those areas as long as bison were present in high enough density to support frequent hunting. As discussed in Section 3.1.1, bison habitat area can vary based on a number of factors including season and forage availability. However, if variables corresponding to bison habitat area can be identified in this study, then, based on the assumption of this model, the inference can be made that human mobility patterns may have mirrored bison mobility patterns. Based on this assumption, variables associated with seasonal bison habitat could also indicate human seasonal landuse patterns and site locations. Additionally, when paired with utility indices, the patch choice model can also be used to identify resource stress based on the degree of faunal processing (Burger et al. 2005). While formal faunal analyses have been limited for the Tanana Valley, this is a potential avenue for future research addressing human-bison relationships

through time and identifying bison population declines.

HBE has also provided a framework for understanding how foraging groups respond to and mitigate risk. In modern foraging cultures, one of the fundamental insurance policies against risk is increased mobility and diversification of resources (Kelly 2013), suggesting that these responses to risk would have also occurred in the past. Risk is an abstract concept that is not only difficult to define, but is also hard to measure, identify, and conceptualize. In archaeology, there are two primary definitions, including "*risk-as-variance*" which equates risk to variability or uncertainty about the outcome of a situation due to uncontrolled parameters (Fitzhugh 2001) and "*probability-of-loss*" which equates risk to the probability of failure and cost of that failure if it happens (Bamforth and Bleed 1997). Risk-as-variance is typically used for research addressing subsistence patterns, and focuses on strategies that seek to prevent or minimize shortfalls in resources. Risk-adverse conditions occur when resources are plentiful and people have a great deal of information about the landscape and how resources could potentially vary. The assumption is that humans will seek to consume the most optimal diet with regards to energy expenditure; however, as unpredictability increases (e.g., decreased abundance of prey, increasing environmental patchiness, drought, etc.), people will begin to incorporate less optimal prey species into their diets, and will also process resources to a higher degree (Burger et al. 2005).

The concept of risk is a useful theoretical perspective as it can provide expectations for decision-making processes and behavioral adaptations to changes in the environment. There is evidence that prehistoric settlement and subsistence patterns shifted during periods of increased environmental variability in Alaska. After the initial florescence between 14,000-13,000 BP, there seems to have been a decrease in site components dating to the Younger Dryas and this has

been interpreted to represent a population decline during this period (Bever 2006; Potter 2008a, 2011; Wygal 2011). The Younger Dryas was a brief cool period when the climate and vegetation returned to more Pleistocene-like patterns in the form of decreased precipitation and increased presence of shrub-tundra (Bigelow and Powers 2001). These patterns suggest that environmental uncertainty and risk-prone conditions were increased during this period. As would be anticipated (based on expectations about risk), there also appears to have been a shift in foraging economies during the Younger Dryas to include a wider spectrum of small game and fish species, while the presence of large-bodied ungulates such as wapiti and bison declined slightly (Potter et al. 2013b). This pattern suggests that bison and wapiti populations may have either shifted their migratory habits and became less predictable, or were not as prevalent on the landscape as during previous periods.

Mobility is another important factor to consider when addressing human-prey relationships and is often addressed through the perspective of risk as increased mobility is considered a key risk-avoidance strategy (Kelly 2013). However, there are many factors that structure mobility, including socio-cultural influence (e.g., Whallon 2006) and environmental aspects (e.g., Kelly 2013). Models of mobility typically incorporate Binford's (1980) definitions of forager vs. collector and residential vs. logistical mobility. Foragers are considered to be residentially mobile and frequently move their camps to food sources, thus having higher mobility overall, while collectors are considered to be logistically mobile and strategize food gathering and bring it back to a centrally-located camp, thus having lower rates of mobility. While these definitions represent a continuum of settlement and subsistence behavior, they do leave different patterns in the archaeological record, and can be helpful for understanding how human behavior may have been organized (see Figure 4 for logistical vs. residential mobility).

Binford (2001) also suggested a generalization between mobility and effective temperature, and found that hunter-gatherers in extreme environments (hot, cold, or dry) have higher degrees of mobility than hunter-gatherers in temperate environments. Additionally, Kelly (2013) noted that a general relationship exists between key subsistence resources and mobility patterns. Groups that rely on marine or aquatic foods typically are more sedentary and logistically mobile, while groups that rely on terrestrial prey typically are more residentially mobile and have larger territory size (Kelly 2013). These observations relating to mobility and settlement patterns are important for understanding human-animal relationships in the past, and suggest that if prehistoric groups in Alaska relied on bison as a primary subsistence resource, they may have had a relatively large territory size but likely organized settlement and subsistence patterns around logistical mobility.

Additionally, the way that bison behavior was organized could have also structured settlement patterns. If bison herds did not migrate on a seasonal basis, but instead were dispersed throughout certain habitat areas, then it is likely that logistical mobility would have been the primary landuse pattern. Bison hunting likely would have occurred on an organized and predictable basis where the herds would have been encountered at short-term hunting camps and transported back to centrally-located residential camps. Additionally, risk would have been low because bison would have represented a predictable and readily available resource that could have been harvested throughout the year.

However, if bison herds did migrate on a seasonal basis, then it would be more likely that residential mobility would have structured settlement and subsistence patterns. Bison were clearly an important subsistence resource. If bison migrated seasonally, humans likely would have structured their movement patterns around the seasonal herd behavior. In a migratory

context, bison would have represented a less-predictable resource throughout the year. However, reliance on them as key subsistence components would necessitate moving residences in concert with the herds. If bison followed this seasonal migratory pattern, it would suggest that subsistence economies during the Late Pleistocene and Early Holocene may have been more specialized that previously thought.

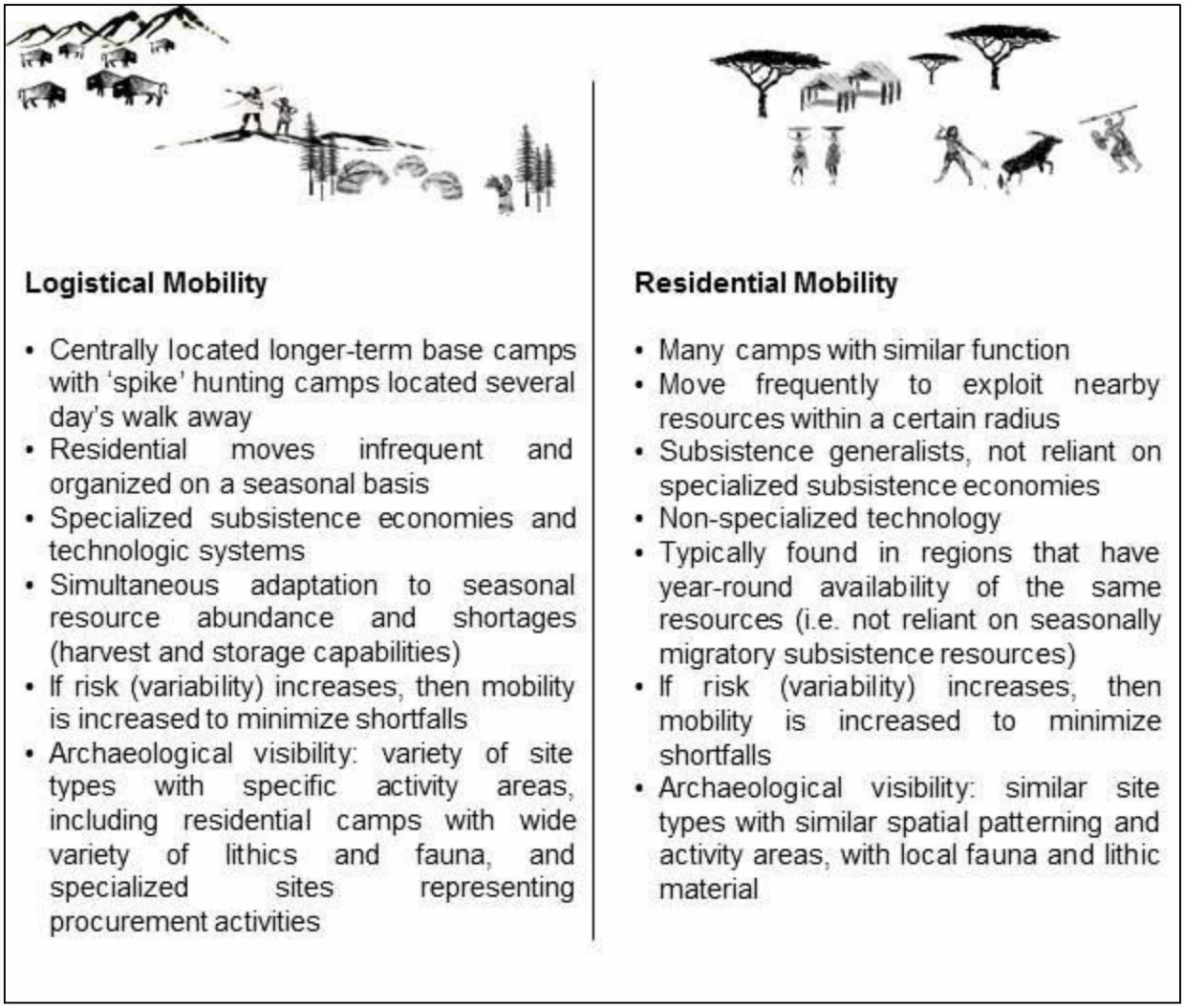

Figure 4. Summary of Logistical and Residential Mobility. Information summarized from Binford (1980), Bousman (2005), Kelly (2013) and Kelly and Todd (1988).

Based on previous research on intra and inter-site spatial patterning, there is already evidence that logistical mobility was practiced during the Late Pleistocene and Early Holocene. The Gerstle River site has been interpreted as a logistically organized short-term bison and wapiti hunting camp where the animals were brought back and processed (Potter 2005, 2007). Utility indices indicate that the low-yield portions of the animals were discarded at the site, while the high utility elements were likely transported off-site to a residential base-camp (Potter 2005, 2007). There is evidence for residential camps at Mead, Upward Sun River, and Broken Mammoth (Potter et al. 2011, 2013a; Krasinski and Yesner 2008; Yesner 2001). Many of the bison faunal remains at Mead and Broken Mammoth are high utility elements, fitting the expectation that the best portions of animals were brought back to the longer-term residential camp from hunting forays within a few days' walk away. This pattern fits the expectation that bison were not seasonally migratory, but instead were dispersed within certain habitats or ecozones, possibly shifting at different times of the year, but likely not migrating long distances on a seasonal basis.

3.3 Summary

Bison were clearly an important component of subsistence economies during the Late Pleistocene and Early Holocene. However, where bison were located, how they moved about the landscape on a seasonal basis, and how they responded to environmental changes remain largely unexplored in Alaskan archaeology. In this study, the Principle of Actualism has provided the theoretical approach for reconstructing bison behavioral ecology based on modern proxies and biomolecular analysis of prehistoric remains. In addition to that, HBE perspectives relating to foraging behavior and settlement structure can be especially informative for understanding

human-bison relationships. In the Tanana Basin there are patterns that suggest logistical mobility was practiced in the past, and was likely embedded within local seasonal resource availability and procurement behavior. Together, these two perspectives suggest that reconstructing the seasonal mobility patterns of steppe bison will provide many inferences for understanding prehistoric human behavior in interior Alaska during the Late Pleistocene and Early Holocene. Steppe bison behavioral ecology is addressed through isotopic analyses, which are discussed in the next chapter.

CHAPTER 4: METHODOLOGICAL APPROACH

Within the past few decades, isotopic analysis has become one of the primary methods for reconstructing the life history of past and present organisms, including diet, environmental factors, migratory behavior, and other aspects (e.g., Bernard et al. 2009; Ezzo et al. 1997; Fox and Fisher 2004; Katzenberg et al. 2012). This study analyzes the isotopic composition of three elements in bison teeth: $^{87}Sr/^{86}S$, $\delta^{18}O$ and $\delta^{13}C$ to reconstruct steppe bison behavioral ecology. Strontium and oxygen isotopes are well-suited for addressing migration and mobility patterns as both isotopes show geographic variability (e.g., Bentley 2006). Strontium in particular is a powerful method for addressing movement patterns because the $^{87}Sr/^{86}Sr$ values in skeletal materials can be linked to geographical places on the landscape (e.g., Ericson 1985; Sealy et al. 1995), almost like a paleo "GPS-chip" that recorded the organism's location. Frequently, $\delta^{18}O$ and $\delta^{13}C$ values are used for environmental reconstruction as $\delta^{18}O$ values record hydroclimatic changes and are useful for characterizing climate (e.g., Gat 1996). $\delta^{13}C$ values can be used to reconstruct the photosynthetic pathways of plants, to determine open vs. closed vegetation regimes, and to identify environmental extremes (i.e., dry/cold, hot/wet, etc.; e.g., Marshall et al. 2007). An overview of stable isotope methods is discussed in the following section, as well as how $^{87}Sr/^{86}Sr$, $\delta^{18}O$, and $\delta^{13}C$ values have been used in this study.

4.1 Isotope Analysis Overview

In some ways, isotopic analysis is a more rigorous and objective method than many traditional methods of archaeological analysis, as it is less susceptible to inter-observer error, subjectivism, or excavation biases than other archaeological datasets. Isotopic analyses provide quantifiable empirical evidence that can be used in comparisons across time and space and is

minimally destructive and can be measured on an array of materials. All organic material (including bioapatite) contains isotopes of different elements, including bones, hair, teeth, muscle tissue, and keratin, as well as soil matrices, hearth residues, leaves, wood, seeds, shells, making isotopic analysis one of the most versatile methods of analysis for biologic systems (Koch 2007). This does not mean isotopic analysis is without methodological biases however, and there are many factors that need to be considered for isotope applications. Hobson et al. (2010) emphasize that three main principles that should always be considered including: 1) understanding the natural distribution and variation of the isotope that is being measured during the time the organism was alive, 2) understanding the discrimination and fractionation processes that can occur between the product and consumer, and 3) understanding the formation processes of the tissue that is being measured. Additionally, studies that apply isotopic analyses to archaeological datasets should always consider contamination and diagenetic factors that could potentially alter isotope values.

Chemical elements are the standard building-block of life, and many of these elements have different isotopic forms, which are simply atoms of a single element that have a different numbers of neutrons. All atoms have a dense nucleus that is composed of protons and neutrons, and an electron cloud that takes up a larger portion of space outside of the nucleus (Peterson and Fry 1987). Atoms of an element that can loose and gain neutrons without fundamentally changing in composition are called stable isotopes. The underlying principle that makes isotopic analysis a useful method for studying biological systems is the supposition that isotopes occur in predictable patterns throughout the natural world, and organisms incorporate isotopes from the surrounding environment into their mineralized tissues through eating, drinking, and respiration processes. When proportions of different isotopes from a single element are measured and

compared, it can provide information about the environmental, physiological, and behavioral factors of an organism.

4.1.1 Standard Notation

A standard notation format for stable carbon and oxygen isotopes has been adopted internationally. The standard notation for stable isotopes of light elements (those with relatively low atomic mass) is expressed in delta (δ) notation (*c.f.*, Peterson and Fry 1987). This allows the values to be comparable spatially, temporally, and across discipline. The following formula is typically used for delta notation and is expressed as δ values in parts per thousand (‰):

$$\delta X(‰) = [(Rsample/Rstandard - 1) \times 1{,}000]$$

where δX is the molar ratio of the heavy to light isotope, *Rsample* is the value of the sample and *Rstandard* is the value of the international standard relative to the isotope that is being measured (Peterson and Fry 1987). Strontium isotope values are typically expressed as the ratio of heavy to light isotopes of that element (i.e., $^{87}Sr/^{86}Sr$).

4.1.2 Fractionation

Most isotopes of atomically 'light' elements (e.g., carbon and oxygen) are affected by fractionation, where the isotope values between the source and product are different. For many skeletal tissues and commonly-analyzed light elements, fractionation occurs in a known and predictable way. Fractionation can be the result of biogenic processes that preferentially incorporate or discriminate between lighter or heavier isotopes of a single element (Ben-David

and Flaherty 2012; DeNiro and Epstein 1981). This process leads to either a decrease (depletion) or an increase (enrichment) in the ratio of heavy to light isotopes between a product and consumer. Metabolic processes in different organisms, different tissue types, and inter-population variation can alter the degree of fractionation as well (Martinez del Rio and Carleton 2012: McCutchan et al. 2003), making it important to have a basis of understanding for the organism and tissue that is the study focus. However, the range of fractionation for most stable isotopes has been established for a majority of tissue types and metabolic processes.

4.1.3 Contamination

As with any biomolecular analysis of skeletal remains, it is important to evaluate contamination issues when applying isotopic methods. A number of studies have established that bone is highly susceptible to contamination and leaching due to its generally porous nature, which exposes it to microbes, water, and extraneous chemicals (*c.f.,* Ben-David and Flaherty 2012; Clementz 2012; Katzenberg 2008). The length of burial, depositional environment, and climate will also affect bone preservation. In addition to this, there are different concerns depending on the element and type of skeletal material that is being measured. Strontium measured in bone material can be especially problematic because it has a similar electron configuration as calcium and bone can absorb the values of the substrate that it is buried in (e.g., Nelson et al. 1986). Hoppe et al. (2003) also found that $\delta^{18}O$ values frequently reset in bone material, even on a Holocene time-scale (i.e., <10,000 years). A number of studies have indicated that treating bone with a weak acid solution can remove surface contamination, but these methods can still lead to variable results and are problematic for studies incorporating bone material (Bentley 2006).

Enamel, on the other hand, is considered the best-preserved skeletal material due to the high density and relatively large size of the crystals, as well as the low organic content. Because of this, dental enamel is relatively resistant to contamination and diagenesis and preserves much better than other skeletal materials. In fact, studies have demonstrated that there is little evidence of contamination or diagenetic alteration in tooth enamel that is several million years old, suggesting that stable isotope values derived from tooth enamel should be considered reliable (e.g., Bocherens et al. 1994; Fox and Fisher 2004; Kohn et al. 1999). Additionally, studies that have focused on analysis of more recent materials (i.e., a Pleistocene-Holocene timescale) have argued that any changes in isotope values due to contamination or diagenesis would be negligible, and should not be a concern for materials in standard depositional environments (Budd et al. 2000; Hoppe et al. 2003).

4.2 Identifying Mobility: Strontium and Oxygen Isotopes

Over the past few decades, strontium and oxygen isotope analysis have been developed as methods for addressing past mobility for both humans and animals. Strontium isotope methods were first applied to the archaeological record by Ericson (1985) and Sealy et al. (1995), who demonstrated that $^{87}Sr/^{86}Sr$ values are incorporated into the inorganic portion of tissue through mineralization processes, and the resulting isotope ratios can be correlated to actual geographical locales. This is because strontium ratios have regional variability resulting from geologic factors, including the elemental composition of the substrate, the age, and weathering processes that it has been subjected to. There are four different isotopes of strontium (^{84}Sr, ^{86}Sr, ^{87}Sr, and ^{88}Sr); however, the isotope that is useful for reconstructing movement is ^{87}Sr, which forms from the radiogenic decay of rubidium (^{87}Rb). Rubidium has a long half-life

of 4.7 x 10^{10} years (Price et al. 2002), and occurs in different proportions depending on the elemental composition of rock material. As it decays, it is released into the surrounding environment as ^{87}Sr, and can also be released by weathering or erosion. These variables affect the ratio of $^{87}Sr/^{86}Sr$ in rock, and lead to a global range of between 0.7000 and 0.8000 (Bentley 2006). Geologic deposits that are very old and had initial high proportions of $^{87}Rb/^{86}Sr$ ratios when the deposit was formed, such as granites, sandstones and shales, will have the highest $^{87}Sr/^{86}Sr$ ratios ranging between 0.7100 and 0.8000. Younger formations or materials that had low proportions of $^{87}Rb/^{86}Sr$ when they formed will have lower $^{87}Sr/^{86}Sr$ ratios, often below 0.7060 (Price et al. 2002; Schwarcz et al. 2010).

Once $^{87}Sr/^{86}Sr$ is released from the substrate it is incorporated into the ecosystem through natural weathering processes, first moving into the soil and water table, and then into the food chain. Strontium has a similar electron configuration to calcium; therefore it is substituted for calcium in the phosphate portion of skeletal structures during the formation and mineralization processes (Bentley 2006). However, because ^{87}Sr is isotopically "heavy", there is no measurable fractionation between the product and the consumer in terms of $^{87}Sr/^{86}Sr$ values, and this has been demonstrated in multiple species and for multiple types of tissues (Hobson et al. 2010). This results in a 1:1 correlation of $^{87}Sr/^{86}Sr$ values between the product and the consumer, which can then be correlated to the geographical area the organism lived in during the formation period of the measured tissue.

For studies that seek to use $^{87}Sr/^{86}Sr$ values to identify geographical affiliation, it is essential to understand the geographical variation of $^{87}Sr/^{86}Sr$ values in the study region in order to compare the specimen to actual physical locations. This is typically accomplished through the use of predictive models, known as isoscapes, which predict isotope variation based on a number

of variables relating to the geologic substrate (the isoscapes used in this study are discussed in Section 5.1). However, the amount of heavy-to-light strontium isotopes that are available on the landscape can be very different from the underlying substrate. Bioavailable ^{87}Sr is typically a mix of many different geologic sources from both alluvial and aeolian transport. Therefore, areas such as river basins will contain a mix of sediments with homogenized $^{87}Sr/^{86}Sr$ values that may be very different from the underlying geology.

The $^{87}Sr/^{86}Sr$ values in hydrologic systems can also be difficult to quantify. The ratios are a reflection of the $^{87}Sr/^{86}Sr$ from water catchment and will be a homogenization of upstream values. Mountainous areas typically have higher values and also erode faster; therefore river water in lowland areas will often have higher $^{87}Sr/^{86}Sr$ values than the surrounding geology. This factor is also dependent on flow rates, and $^{87}Sr/^{86}Sr$ values can, in some situations, fluctuate between periods of high and low water in river systems (Aubert et al. 2002; Douglas et al. 2013). Similarly, the depth of the water table also affects values for all terrestrial water sources. Douglas et al. (2013) found that in regions of permafrost where the water table shifted depths seasonally, $^{87}Sr/^{86}Sr$ values varied significantly. This last factor is a concern for circumpolar studies addressing migration, as a difference in $^{87}Sr/^{86}Sr$ values could result from freeze-thaw cycles, rather than changes in geographical location. However, Britton et al. (2009) found that $^{87}Sr/^{86}Sr$ in modern caribou tracked very well with known migration patterns, and my research also incorporates a control study of modern bison to assess how $^{87}Sr/^{86}Sr$ values track with well-known migration patterns in the Tanana Valley region (see Chapter 6).

Oxygen isotopes are another well-suited method for reconstructing migration and mobility patterns, and are often used in conjunction with $^{87}Sr/^{86}Sr$ values to identify seasonality. $\delta^{18}O$ values reflect environmental water sources, but can be used in a similar way as strontium

isotopes for identifying mobility. Oxygen has three stable isotopes, ^{16}O, ^{17}O, and ^{18}O, but only ^{18}O and ^{16}O isotopes are used for deriving $\delta^{18}O$ values. Oxygen stable isotopes follow standard delta notation and are expressed relative to the international standard, Vienna Standard Mean Ocean Water (V-SMOW) which has a value of 0‰. Variation in $\delta^{18}O$ values results from global condensation/precipitation cycles of meteoric water and has a global variation of approximately ~110‰ (Gat 1996). The ocean is the source of the meteoric water cycle and $\delta^{18}O$ ratios in ocean water have a value of around 0‰. When ocean water is condensed into clouds, the water retains that ratio of approximate 0‰, but as the clouds begin to move across landmasses, discrimination between the heavy (^{18}O) and light (^{16}O) oxygen isotopes occurs, resulting in a gradient of $\delta^{18}O$ across landmasses that decreases with distance from the source. In rain clouds, the heavier isotopes (^{18}O) are typically precipitated first, leaving a greater proportion of the lighter isotopes (^{16}O) which results in a variation of $\delta^{18}O$ values based on increasing latitude, altitude, distance from coast, seasonality, and decreasing temperature (Bowen et al. 2005).

Oxygen isotopes are incorporated into the body by ingesting water, but the process is related to several factors. In terrestrial mammals, oxygen is incorporated into the body in multiple ways. Greater than 50% of the uptake of oxygen into the body is related to diet and water, but about 25% is incorporated though atmospheric oxygen gas and about 15% from water vapor (Koch 2007). This means that $\delta^{18}O$ values in an organism can be an average derived from multiple sources and biogenic processes. Additionally, $\delta^{18}O$ values in vertebrates can vary based on feeding behavior as the leaves of plants are often enriched in ^{18}O relative to stem portions, and $\delta^{18}O$ values also increase with canopy height (Koch 2007). Unlike strontium, which has no measurable fractionation, oxygen isotopes are fractionated between source and product, and this process is dependent on body temperature (Longinelli 1984; Luz and Kolodny 1989). However,

Hoppe (2006) demonstrated that in modern bison, there is a close relationship between $\delta^{18}O$ values in carbonate and local surface water, and derived the following regression formula:

$$\delta^{18}O_{carbonate} = 30.06(\pm 1.40) + [0.70(\pm 0.12) * \text{Mean } \delta^{18}O_{water}]$$

This relationship would have assumedly been the same for paleo-bison as well (Hoppe 2006), meaning that $\delta^{18}O$ values in the carbonate portions of bison remains reflect the water that the bison ingested.

Oxygen isotopes are also especially useful for identifying seasonality. Seasonal fluctuation of $\delta^{18}O$ values occurs in a predictable pattern in northern latitudes due to the variation of values from rain vs. snow. When plotted, this variation is represented as a sinusoidal wave varying between high $\delta^{18}O$ in the winter and low $\delta^{18}O$ in the summer (Bernard et al. 2009; Fricke et al. 1998). Pairing $\delta^{18}O$ values with $^{87}Sr/^{86}Sr$ values is an especially useful method for identifying changes in geographical location based on seasonality. However, identifying seasonal migration patterns requires an understanding of the physiological development for different skeletal tissues, as well as specific sampling techniques. These factors are discussed in Section 4.4.

4.3 Identifying Climate and Seasonality: Carbon and Oxygen Isotopes

Carbon and oxygen isotopes are often used together for environmental reconstructions. There are three naturally occurring carbon isotopes, including ^{12}C, ^{13}C, and ^{14}C. $\delta^{13}C$ values are derived by measuring the ratio of ^{13}C to ^{12}C isotopes, relative to the international standard of Vienna Pee Dee Belemnite (Ben-David and Flaherty 2012). The global range of $\delta^{13}C$ for

vertebrate species ranges between -60 and +5‰ (Koch 2007), and are dependent on environment and diet. One caveat to interpreting $\delta^{13}C$ (and is especially important for studies that incorporate modern samples) is that atmospheric CO_2 has steadily increased since the Industrial Revolution and has led to a bias towards more negative $\delta^{13}C$ values (Ben-David and Flaherty 2012).

Carbon stable isotopes are frequently used for dietary reconstruction because the carbon values in skeletal tissues are derived from food sources, and show variation based on the types of foods that were consumed. However, because diet can also be reflective of environmental factors, carbon isotopes can also be used as a proxy for environmental reconstructions. Carbon in herbivores is largely derived from plant sources, and $\delta^{13}C$ values in the skeletal tissues of mammalian herbivores will reflect the photosynthetic pathway of the plants that were consumed. There are two dominant photosynthetic pathways in plants, known as C_3 and C_4 pathways, which differ in how ^{13}C isotopes are fractionated against during the fixation of CO_2 (Marshall et al. 2007).

This process causes a variation in $\delta^{13}C$ values between the two pathways. Plants with C_3 pathways typically have values of around -26‰ and are found throughout temperate, northern, and arctic regions. Alaska almost exclusively has plants with C_3 pathways (Wooller et al. 2007). Plants with C_4 pathways have values of around -12‰, and are found in equatorial and some temperate regions (Lee-Thorpe 2008; Marshall et al. 2007). The $\delta^{13}C$ values of the two photosynthetic pathways are not static however, and vary based on environmental factors. Plants with C_3 pathways typically show the most variance based on climate, with the lowest $\delta^{13}C$ values in closed canopy vegetation or in wet or cold regions, while C_3 plants in open habitats or in arid regions typically have the highest $\delta^{13}C$ values (Marshall et al. 2007). Therefore, by measuring $\delta^{13}C$ values in herbivore species local environments can be reconstructed and compared.

Similar to oxygen isotopes, fractionation is a factor to consider for $\delta^{13}C$. Bone collagen has a fractionation range of between -1.5‰ to +2.7‰ with a mean of about +0.8‰ (DeNiro and Epstein 1978); however a fractionation value +1‰ for bone collagen is frequently cited in the literature (Ben-David and Flaherty 2012). Additionally, the exact fractionation value can differ depending on the organism and tissue being analyzed (*c.f.,* Martinez del Rio et al. 2009). Dental enamel is not frequently analyzed for $\delta^{13}C$ values; however, the fractionation of both the carbonate and phosphate portions of bioapatite has been determined to be approximately +14‰ for terrestrial ungulates (Balasse 2002; Cerling and Harris 1999; Passey et al. 2005). Unfortunately, there have been no *Bos*-specific studies on carbonate-derived stable carbon isotope fractionation, but the increase of 14‰ is frequently cited in the literature (e.g., Balasse 2002; Cerling and Harris 1999; Passey et al. 2005), and will also be used for this study.

Oxygen isotopes are also useful for environmental reconstructions due to temporal variation in $\delta^{18}O$ values, which can occur on seasonal as well as long-term climactic scales. As discussed previously, seasonal fluctuations of $\delta^{18}O$ values occur in northern latitudes with high values in winter and low values in summer (e.g., Fricke et al. 1998). Long-term variation in $\delta^{18}O$ values can also be used to investigate global climate change (e.g., Dansgaard et al. 1969). During periods of glaciation, a large portion of water is removed from the meteoric water cycle in the form of glaciers (*c.f.,* Miller et al. 2010). Due to fractionation processes, a high volume of ^{16}O is locked away in the form of ice which then causes the ocean to have a proportionally higher amount of ^{18}O and is reflected as more positive $\delta^{18}O$ values during glacial periods (Gat 1996). Climate-induced variation in global $\delta^{18}O$ typically results in a small change in values - on the scale of 1-2‰ – however, it is enough to act as a global 'paleo-thermometer', and has been the predominant method for measuring global climate change in ice cores (*c.f.,* Barnola et al. 1987).

4.4 A Cautionary "Tail": The Importance of Physiology in Isotope Applications

Formational processes and differential turn-over rates are important to consider for any isotopic studies. Bone has the same basic physiological properties in all mammalian species and remodels throughout the lifespan of the individual (*c.f.,* Katzenberg 2008). Therefore, isotopes measured on bone will represent a homogenization of values over the past several years of the individual's life. Dental enamel on the other hand does not remodel once it is formed, essentially trapping isotope values from that period of formation and development (*c.f.,* Katzenberg 2008). This makes dental enamel well-suited for addressing change over time in isotope values within single individuals. Bones and teeth are often analyzed together in studies of human migration because they present different 'windows' of time from the individual's life, and can indicate if there were changes over time in geographical affinity between when teeth formed (childhood) and when bone material formed (adulthood). In contrast, ungulate teeth are often used for migration studies because the enamel portion forms in sequentially mineralized layers. Ungulate teeth are often used to address intra-individual change over time as isotope values are sequentially trapped in the enamel for short developmental stages of the animal's life. This approach is called time-series isotopic studies or serial-sampling (see Figure 5 for reference) and has greatly improved our understanding of paleo-behavioral ecology for many species (e.g., Balasse and Ambrose 2002; Britton et al. 2011; Feranec et al. 2009; Fisher and Valentine 2013; Gadbury et al. 2000; Hedman et al. 2009; Higgins and MacFadden 2004; Julien et al. 2012; Metcalf et al. 2010; Pellegrini et al. 2008; Porder et al. 2003).

While the composition of dental enamel is similar for all vertebrates, the formation processes differ slightly between species. Dental enamel is one of the densest skeletal materials, and when completely formed, is composed of ~96% inorganic material (hydroxyapatite) and

<1% of organic material (the remaining portion is composed of water in living organisms; Williams and Elliott 1989). The basic process of dental enamel formation begins when thin lamellar bands of hydroxyapatite are secreted by ameloblasts (Hillson 1996). This process starts at the crown of the tooth and then moves outward and downward to the cemento-enamel junction (CEJ), meaning that the top of the tooth represents the oldest enamel, and the enamel near the roots is the youngest (Hillson 1996). When it is first secreted, enamel is not fully mineralized

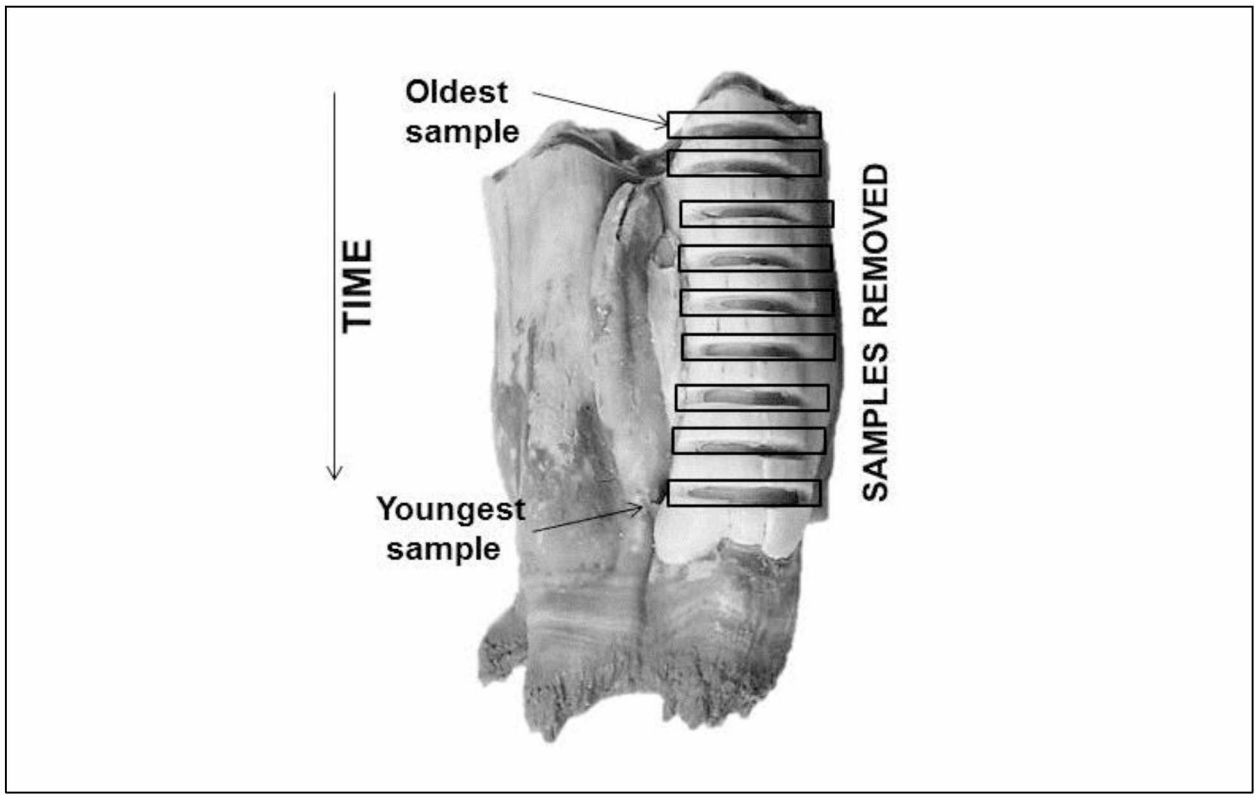

Figure 5. Example of Serial-Sampling Technique. This picture demonstrates serial-sampling techniques on steppe bison M_2 that has a development period of approximately 13 months. The oldest sample would have formed around the 1st or 2nd month of life, while the youngest sample would have formed around the 14th month of life (Gadbury et al. 2000).

and requires weeks to months to fully harden and mature. However, once this process iscomplete the enamel does not remodel. The mineralization process also differs between species. In humans, the mineralization process happens more or less at the same time and a single tooth will contain homogenous isotope values throughout, regardless of where a sample is removed (*c.f.,* Montgomery and Evans 2006). The process is a somewhat different in ungulates, and enamel forms and mineralizes incrementally over a year or more, trapping isotope values that correspond to different periods of the individual's life (Wiedemann et al. 1999).

Serial-sampling ungulate teeth is a well-established method and has been applied to many studies of ungulate mobility, including European steppe-bison (Julien et al. 2012), Holocene plains bison (Widga et al. 2010), Pleistocene-aged caribou and bison from France (Britton et al. 2011), Pleistocene-aged horse and bison from the Sonoran Desert (Higgins and MacFadden 2004) and modern radio-collared caribou in Alaska (Britton et al. 2009). Second and third molars (M_2/M_3) are typically the teeth that are chosen for time-series isotopic studies on ungulates because they have the longest growth period and both teeth encapsulate over a year's worth of growth. In bison, second molars begin forming about a month after birth and complete formation around the fourteenth month of life. Third molars begin forming around the ninth month of life, and complete formation at around two years, encompassing about fifteen months of growth (Brown et al. 1960; Gadbury et al. 2000). Because bison demonstrate reproductive synchronicity (i.e., calves are always born in the spring) tooth eruption and growth can be correlated to a seasonal and even monthly basis (Figure 6).

However, while dental eruption can be correlated on a monthly basis, it can take several weeks to months for enamel to fully mineralize and harden. This means that the isotope ratios trapped in the enamel will represent a homogenization of values, making it difficult to associate

isotope values from certain portions of the tooth to short periods of time such as weeks or months (Balasse 2002; Bentley 2006; Zazzo et al. 2006). Some researchers caution that even

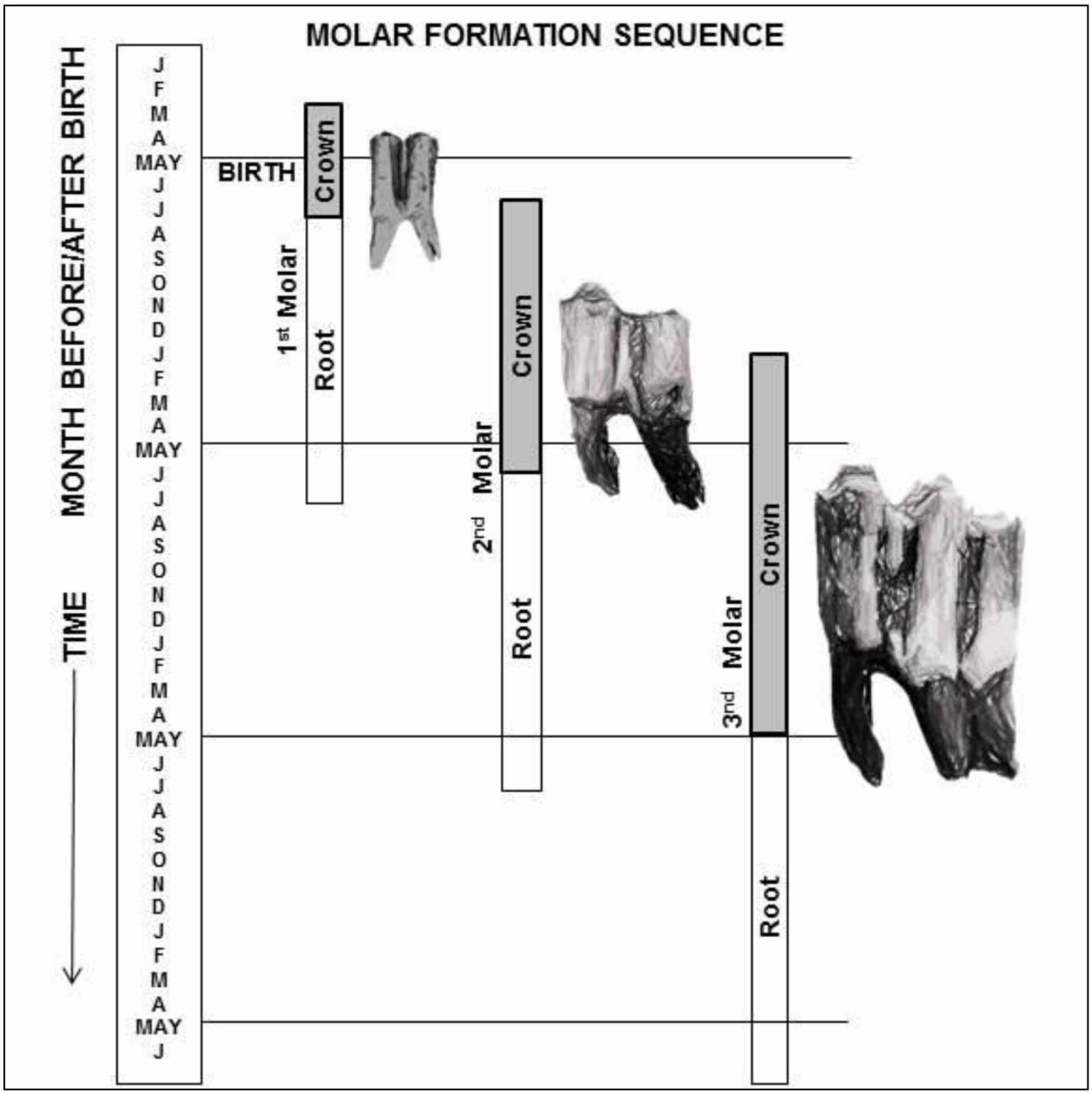

Figure 6. Timing of Bison Molar Formation. Bison molars form between approximately two months prior to birth to 37 months after birth, effectively capturing three years of growth and development. Modified from Gadbury et al. (2000).

assigning seasonality to serial-samples can be problematic (i.e., Balasse 2002), but most researchers applying time-series isotopic sampling assign season (e.g., Bernard et al. 2009; Britton et al. 2011; Feranec et al. 2009; Higgins and MacFadden 2004; Julien et al. 2012; Koch et al. 1989; Pellegrini et al. 2008; Widga et al. 2010).

Oxygen isotopes show seasonal variation and are often used to determine what portion of a tooth represents summer vs. winter. Julien et al. (2012) used this approach to reconstruct the seasonal movement patterns of Pleistocene-aged *Bison pricus* from Ukraine. Instead of attempting to correlate rate-of-growth with location on the tooth and account for inter-population variation in physiology and development - an arguably imprecise process - the researchers used the peaks and troughs of the $\delta^{18}O$ values of each individual to represent the peak yearly warm and cool periods (Julien et al. 2012). This method provided a way to assess seasonal inter-population variation in isotope values. Analyzing oxygen isotopes in conjunction with other isotopes removes potential sources of error that could result from attempting to correlate rate-of-growth with the isotope values. The $\delta^{18}O$ values in this study will help to determine peak warm/cool seasons in this study.

4.5 Summary

Stable isotope analysis is a useful method for reconstructing life-histories. It is especially important for studies in archaeology as it provides a means to address many aspects of past lifeways that would be difficult to address through any other method. This study specifically applies $^{87}Sr/^{86}Sr$, $\delta^{18}O$, and $\delta^{13}C$ analysis to serially-sampled steppe bison teeth to reconstruct seasonal movement patterns and other aspects of behavioral ecology. Strontium and oxygen isotopes are often used in migration studies because they show regional variation. Strontium in

particular can be associated with specific geographical locations, making it a powerful way to identify landuse patterns, and will be used in this study to identify bison mobility. Oxygen isotopes will be used to identify seasonality, as well as changes in altitudinal or latitudinal locations, while carbon isotopes will be used to indicate diet and environmental context. The next chapter discusses the specific materials, site locations, and laboratory methods used in this study.

CHAPTER 5: MATERIAL AND METHODS

The primary goals of this study are to reconstruct the seasonal migratory behavior of steppe bison, to determine if bison were associated with certain physical features on the landscape, and to explore whether mobility patterns changed over time. This was accomplished by collecting multiple samples of dental enamel from individual bison teeth, and then analyzing the samples for $^{86}Sr/^{87}Sr$, $\delta^{18}O$, and $\delta^{13}C$. A total of 106 samples were removed from 14 prehistoric steppe bison teeth from the YTU and chemically processed to remove contamination before being analyzed in designated isotope facilities. In addition, 27 samples from three modern bison teeth were also collected and processed using the same methods. The modern teeth are used here as control samples to provide information about $^{86}Sr/^{87}Sr$ and $\delta^{18}O$ in bison teeth from the Tanana Valley with known behaviors, and will be discussed in more detail in Chapter 6. An additional component that has been essential for interpreting the isotope results is the use of GIS-derived models of isotope variability for Alaska (Bataille et al. 2014; Sloat 2014), as these models have provided predicted values of $^{87}Sr/^{86}Sr$ and $\delta^{18}O$ values for the site locations.

5.1 Modeling Strontium and Oxygen Variation in the Tanana Valley

To be able to apply strontium and oxygen isotope data to migration studies, it is necessary to have an understanding of the geographical variability of those isotopes in the region of study. This is often done by creating GIS models, known as isoscapes, which predict the geographical distribution and variability of isotope values for large geographical areas (West et al. 2010). Isoscapes are typically developed by plotting a distribution of sample values with GIS software, and then extrapolating values for the rest of the study area based on environmental, geologic, or climatic variables. These methods have been used to model the distribution of

$^{87}Sr/^{86}Sr$ and $\delta^{18}O$ values for several regions in North America (Bataille and Bowen 2012; Beard and Johnson 2000; Bowen et al. 2005; Chesson et al. 2012; West et al. 2010), and provide a powerful tool for geospatial analysis of isotope values.

5.1.1 Strontium Isoscape

This study uses a predictive model of $^{87}Sr/^{86}Sr$ values for Alaska that was developed by Bataille et al. (2014) based on bedrock composition, geologic age, and ^{87}Rb chemical weathering for the geologic terrains in Alaska. This is the first strontium isoscape to be developed for Alaska, and is based on the global lithological map (GLiM) developed by Hartmann and Moosdorf (2012). Bataille et al. (2014) created the bedrock model using multiple sub models, including separate ones for igneous and siliciclastic rocks, by using Monte Carlo simulations. The raster datasets for the sub-models were then mosaiced to derive minimum, maximum, median, and 1st and 3rd quartiles for $^{87}Sr/^{86}Sr$ across the entire surface of Alaska (Bataille et al. 2014). The resulting isoscape model was then validated with 97 samples of sedimentary rocks and 788 samples of igneous rocks throughout the state. The bedrock model explained 72% of the observed variation in igneous rock but only 51% of the variation in sedimentary rocks (Bataille et al. 2014).

The chemical weathering model developed by Bataille et al. (2014) was created using multiple linear regression of several data sources, including mean annual runoff from the Global Runoff Data Center dataset, the mean annual temperature from the WorldClim dataset, and mean slope from digital elevation datasets (see Bataille et al. 2014 for references). The resulting model was calibrated by comparing the results to 339 published samples of $^{87}Sr/^{86}Sr$ from Alaskan rivers. Additionally, the authors created a catchment model to predict $^{87}Sr/^{86}Sr$ in

Alaskan watersheds that combined the bedrock and chemical weathering models. The catchment model was validated using samples collected by Brennan et al. (2014) from 61 Alaskan rivers. Eighty-nine percent of the sample values fell within the interquartile range of the prediction. Interestingly, three rivers in the YTU - the Chena, Salcha, and Chatanika Rivers - did not perform well; removing these rivers (along with the Nenana River) allowed the catchment model to explain 82% of the variance for the entire state. The rivers in the YTU actually have higher $^{87}Sr/^{86}Sr$ values than the model predicted. The authors suggest that the amount of silicate-derived metamorphic units in this region have a much higher contribution than the model predicts, or that metamorphosed limestones and marbles contribute to the discrepancy. The model parameters did not distinguish between types of metamorphic rock; however, the presence of marble or metalimestone, which have variable rates of weathering, could alter the observed values (Bataille et al. 2014).

While this model does not perfectly represent the bioavailable $^{87}Sr/^{86}Sr$ for the study region, it was created using the best available methods, and is the only attempt to date to map strontium isotope variability in Alaska (Bataille et al. 2014). While rivers in the YTU seem to show greater variability than the model predicted, it can still be used as a method for associating $^{87}Sr/^{86}Sr$ values from the samples in this study to actual geographical locations. Additionally, the model was created using 1000 m resolution DEM rasters, and shows very high resolution compared to other studies that have modeled $^{87}Sr/^{86}Sr$ distribution for migration studies (e.g., Bentley 2004; Britton et al. 2009; Britton et al. 2011; Haverkort et al. 2008; Julien et al. 2012; Thornton 2011).

5.1.2 Oxygen Isoscape

This study also utilizes a $\delta^{18}O$ isoscape produced for the state of Alaska by Sloat (2014; Figure 7). The isoscape was created for surface waters based on 400 water samples collected across Alaska and the Yukon. The samples demonstrated that winter temperature and precipitation affected $\delta^{18}O$ values the most, resulting in the highest $\delta^{18}O$ values along the Gulf of Alaska, and the lowest values inland towards interior Alaska. The isoscape was derived through 300m resolution DEM datasets in ArcGIS, including mean annual temperature, winter average temperature, summer annual temperature, mean annual precipitation, cumulative mean annual precipitation, winter precipitation, summer precipitation from the WorldClim dataset (Hijmans et al. 2005). The results modeled the relationships of surface water $\delta^{18}O$ values, winter precipitation, and winter mean temperatures at 30-arc-seconds, demonstrating high resolution. The resulting isoscape (Figure 7) shows estimated values for the YTU and Tanana Basin of between -19.0‰ and -24.0‰, with higher values in mountainous areas, and lower values in valleys and basins.

Sloat (2014) also derived a formula for determining past temperature ($\delta^{18}O$-T) relationships and found that there is an approximate 0.55‰ increase in $\delta^{18}O$ values with each 1°C increase in mean annual temperature. This suggests that $\delta^{18}O$ for steppe bison during the Pleistocene would be expected to be much higher, but would vary in a similar way to modern values. Schneider von Deimling et al. (2006) estimate that during peak stadial periods, the average global temperature would have been 5-10°C colder. By applying the regression formula derived by Sloat (2014), it can be estimated that $\delta^{18}O$ values would have increased between 2.75-5.5‰ during the LGM and other stadial periods.

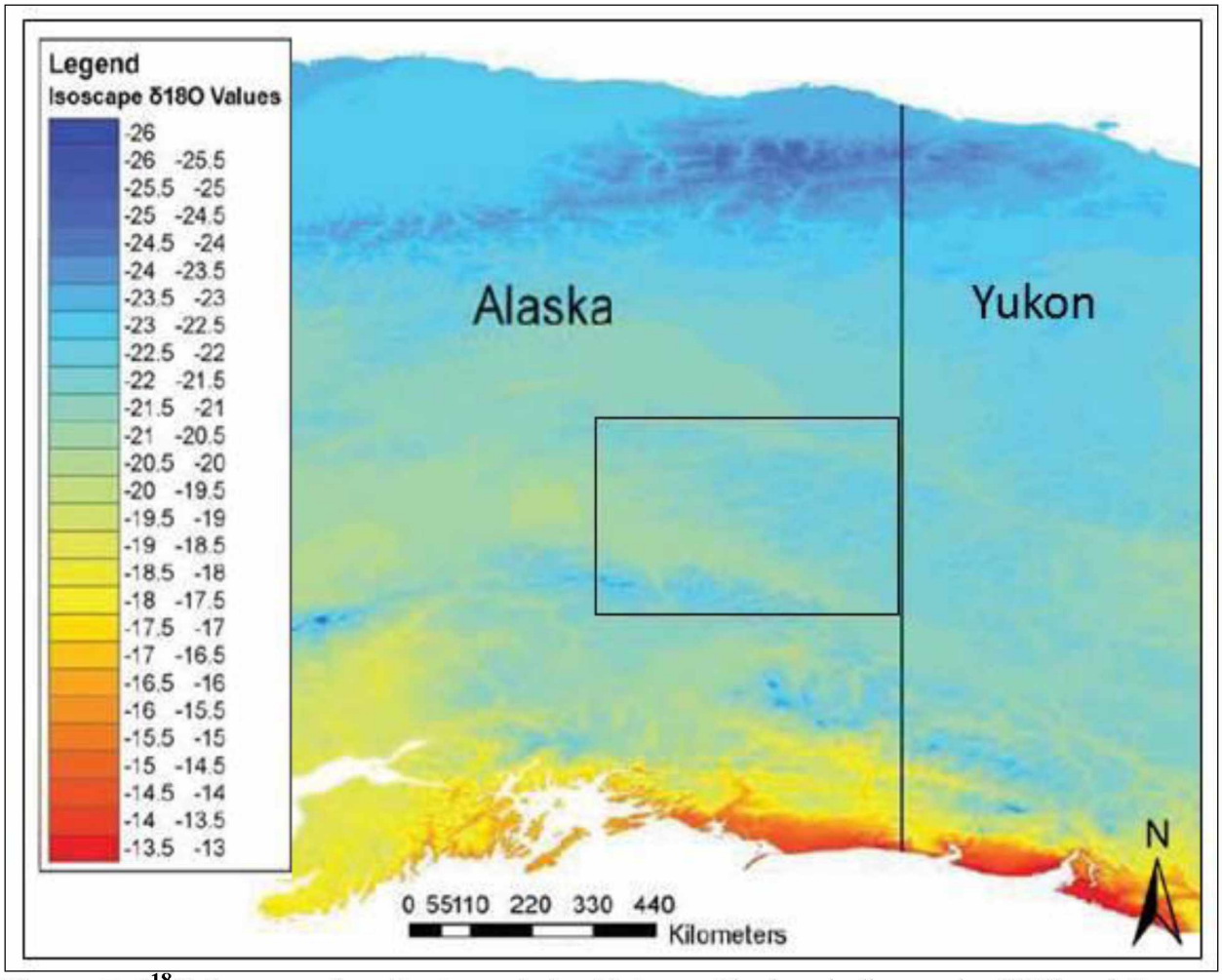

Figure 7. $\delta^{18}O$ Isoscape for Alaska and the Yukon. The box indicates the YTU and Tanana Basin. Modified from Sloat (2014).

5.2 Sample Collection and Site Descriptions

The prehistoric bison teeth used in this research (n = 14) came from two sources (see Table 1 for the list of specimens and Figure 8 for a map of the locations): the U.S. Army Corps of Engineers Cold Research and Engineering Laboratory (CRREL) near Fairbanks (locally known as the "Fox Permafrost Tunnel") and the Lost Chicken Creek paleontological collection, originally collected near Chicken, Alaska in the Forty Mile Mining District and now housed at the University of Alaska Museum of the North in the Earth Sciences Department. The modern

samples used in the control study are from the Delta Bison Herd, which resides in the Tanana and Delta River valleys near Delta Junction.

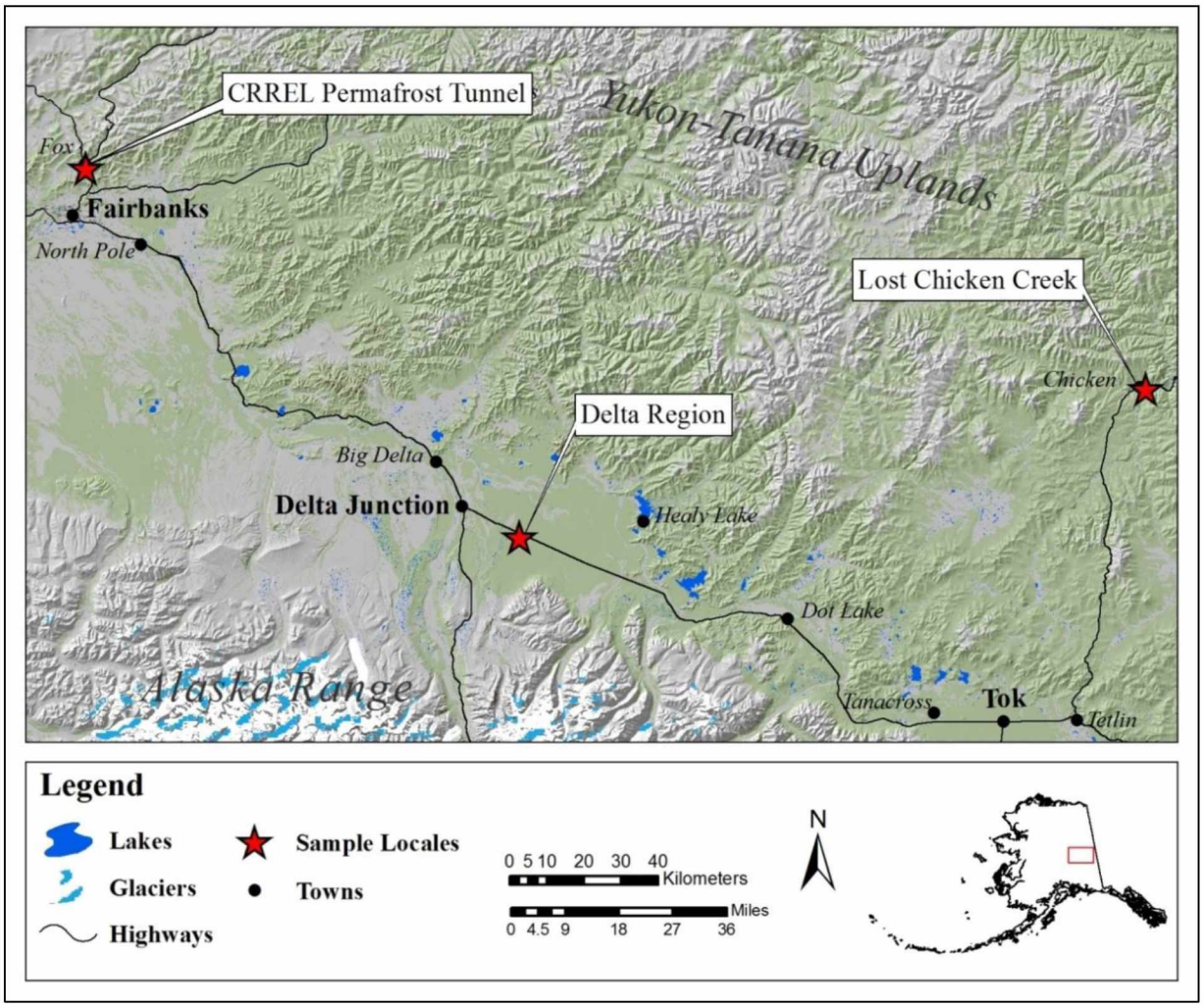

Figure 8. Map of Sample Locales. Red stars show the locations of where the samples were collected from for this study. The CRREL Permafrost Tunnel and Lost Chicken Creek are the prehistoric sample locales, while the Delta Region label shows the general range of where the modern bison samples were collected from.

Table 1. List of specimens used in this study.

Collection	Specimen ID	Locale	Tooth	# Samples Removed
CRREL	FPT	Fox Permafrost Tunnel	M_3	6
UAM Earth Science	UAMES-6335	Lost Chicken Creek	M_3	7
UAM Earth Science	UAMES-6173	Lost Chicken Creek	M_2	8
UAM Earth Science	UAMES-6768	Lost Chicken Creek	M_2	8
UAM Earth Science	UAMES-6377	Lost Chicken Creek	M_3	11
UAM Earth Science	UAMES-6602	Lost Chicken Creek	M_3	8
UAM Earth Science	UAMES-6620	Lost Chicken Creek	M_3	9
UAM Earth Science	UAMES-6616	Lost Chicken Creek	M_3	8
UAM Earth Science	UAMES-6785	Lost Chicken Creek	M_3	7
UAM Earth Science	UAMES-12224	Lost Chicken Creek	M_2	6
UAM Earth Science	UAMES-6382	Lost Chicken Creek	M_3	6
UAM Earth Science	UAMES-8582	Lost Chicken Creek	M_3	6
UAM Earth Science	UAMES-6594	Lost Chicken Creek	M_3	8
UAM Earth Science	UAMES-6599	Lost Chicken Creek	M_3	7
AK Dept. Fish & Game	DH1a	Delta Bison Range	M_2	8
AK Dept. Fish & Game	DH1b	Delta Bison Range	M_3	8
AK Dept. Fish & Game	DH2	Delta Bison Range	M_3	11

5.2.1 Fox Permafrost Tunnel

A single specimen (labeled as FPT) in this study came from a steppe bison mandible that was found during construction of the CRREL Permafrost Tunnel (U.S. Army Corps of Engineers 2012). The Permafrost Tunnel is located in a thick sediment deposit near the confluence of Goldstream and Glenn Creeks in the Goldstream Valley near Fox, approximately 15 miles north of Fairbanks. The Permafrost Tunnel was first excavated in the 1960s for the purpose of understanding permafrost and permafrost environments, and has remained a source of ongoing research focusing on artic climate change, cold-weather engineering, and Pleistocene-aged environmental reconstructions (U.S. Army Corps of Engineers 2012).

The underlying geology in the vicinity of the CRREL Permafrost Tunnel (~100 km radius) is primarily composed of Paleozoic age quartzites and quartz schists of greenschist and amphibolite facies (known as the Birch Creek Schist formation), along with a scattering of granitic plutions, marble, and eclogite formations (Foster et al. 1994). Additionally, calcareous phyllite and quartose mylonitic schist of an unknown age are present to the south (Foster et al. 1994). As previously discussed in Section 4.2, geologic age, elemental composition, and weathering processes all contribute to a variation in $^{87}Sr/^{86}Sr$ values. The geology in the region surrounding the Permafrost Tunnel has a predicted $^{87}Sr/^{86}Sr$ values range of between 0.7058 and 0.7646 (Figure 9; Bataille et al. 2014). The predicted $^{87}Sr/^{86}Sr$ values from the YTU catchment model derived by Bataille et al. (2014) did not always have a strong correlation to measured samples, and the Chena River is an especially problematic region (2014). Bataille and colleagues suggested that this was due to homogenous characterization of the underlying geology of the region, which did not account for small deposits of sources with higher $^{87}Sr/^{86}Sr$ values (2014). Measured values on water samples, at least for the Chena River, show higher values than predicted by the model and suggests that values for bioavailable strontium may be higher as well (Bataille et al. 2014).

The stratigraphy at the CRREL tunnel is approximately 20 m thick and is composed of silt and gravel deposits overlaying Birch Creek Schist that were deposited from alluvial and eolian sources (Sellmann 1967). The primary deposit of faunal remains was found at a depth of 10 m below surface in the Goldstream Formation, which was deposited from alluvial sources and solifluction processes during the Late Wisconsin Glaciation (between 25,000 and 19,000 years BP). The Goldstream Formation shows evidence of climatic change, and dating of organic material in the ice wedges indicates that the lower one formed during the LGM when climates

were much colder and dryer (U.S. Army Corps of Engineers 2012; Wooller et al. 2007). The higher ice wedge dates to the Pleistocene-Holocene transition, and suggests that a warming period melted permafrost deposits prior to the formation of the second wedge. This warming period has been termed the Fox Thermal Event and is thought to be a localized event (Hamilton et al. 1988). Faunal remains from several species, including the bison tooth used in this study, were found in the sediments between the two ice wedge formations, and date to ~14,500 BP.

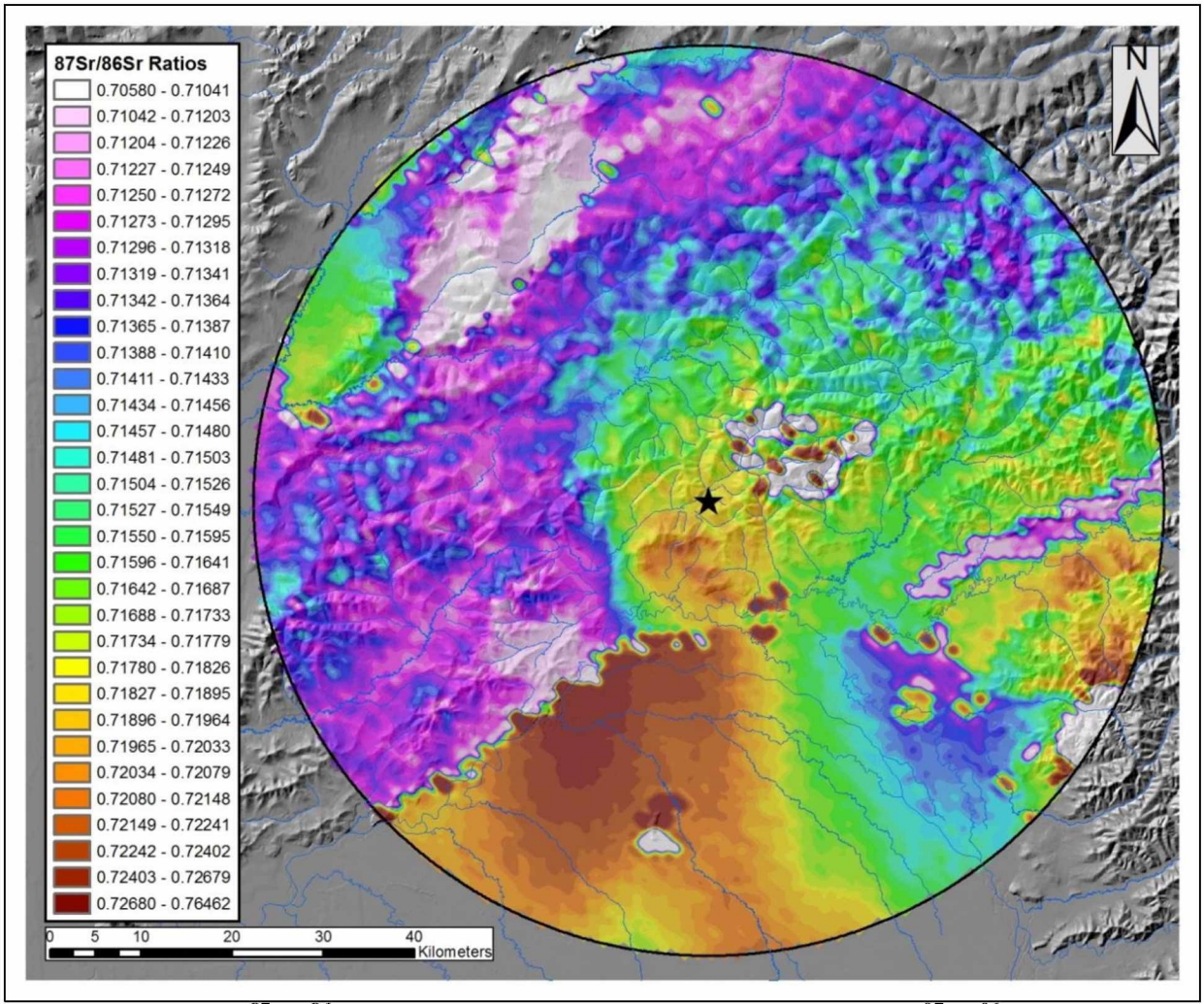

Figure 9. CRREL $^{87}Sr/^{86}Sr$ Isoscape. This map shows the variation in $^{87}Sr/^{86}Sr$ values in a 50 km radius from the CRREL Permafrost Tunnel (represented by the black star). Derived from the Bataille et al. (2014) raster dataset.

5.2.2 Lost Chicken Creek

The other thirteen prehistoric specimens used in this study (see Table 1) were from a paleontological deposit discovered by placer mining activities at Lost Chicken Creek in the Forty Mile Mining District. Lost Chicken Creek is a small tributary of the Fortymile River and is located in the YTU in east-central Alaska near the Canadian border. The stratigraphic deposits at Lost Chicken Creek have yielded thousands of specimens of at least 16 genera of Pleistocene mammal species, along with invertebrate and plant macrofossils (Porter 1988), and represents a valuable source of information for paleoecological research in east-central Alaska.

The YTU are a mountainous region located between the Tanana River to the south, and Yukon River to the north. The underlying geology for the region is composed of intrusive felsic rock of Cretaceous age, metamorphic rock of Precambrian and Paleozoic age, and Jurassic-age granitic intrusions (Beikman 1980). The surficial geology is composed of Tertiary and Quaternary fluvial, colluvial, and eolian deposits (Foster et al. 1994). Several sediment basins are scattered throughout the Yukon-Tanana Uplands, and there is a small sediment basin of lower Tertiary age located in the Lost Chicken Creek region (Foster et al. 1994). As previously discussed in Section 4.2, geologic age, elemental composition, and weathering processes all contribute to a variation in $^{87}Sr/^{86}Sr$ values. The geology in the Lost Chicken Creek vicinity (50 km radius) has a predicted $^{87}Sr/^{86}Sr$ values range of between 0.7039 and 0.7111 (Figure 10). The range for watershed systems is predicted to be slightly higher (Bataille et al. 2014), and likely represents more accurate values for bioavailable strontium.

There has been active mineral exploration in the Lost Chicken Creek region for over a century and it was through placer mining activities that many faunal remains, including the bison teeth used in this study, were uncovered in frozen silt and muck deposits along the creek banks.

The discovery and collection of Pleistocene-aged faunal materials exposed by mining has a long history in interior Alaska (*c.f.*, Guthrie 1968), and, in the 1970s and 1980s, the Bureau of Land Management (BLM) developed a collaborative program with local miners in the Fortymile and Circle Mining Districts where the miners would collect and pile up any bones that were exposed, and BLM would come and collect the skeletal materials for curation at the University of Alaska Museum of the North in the Earth Sciences Department. Unfortunately, no information about

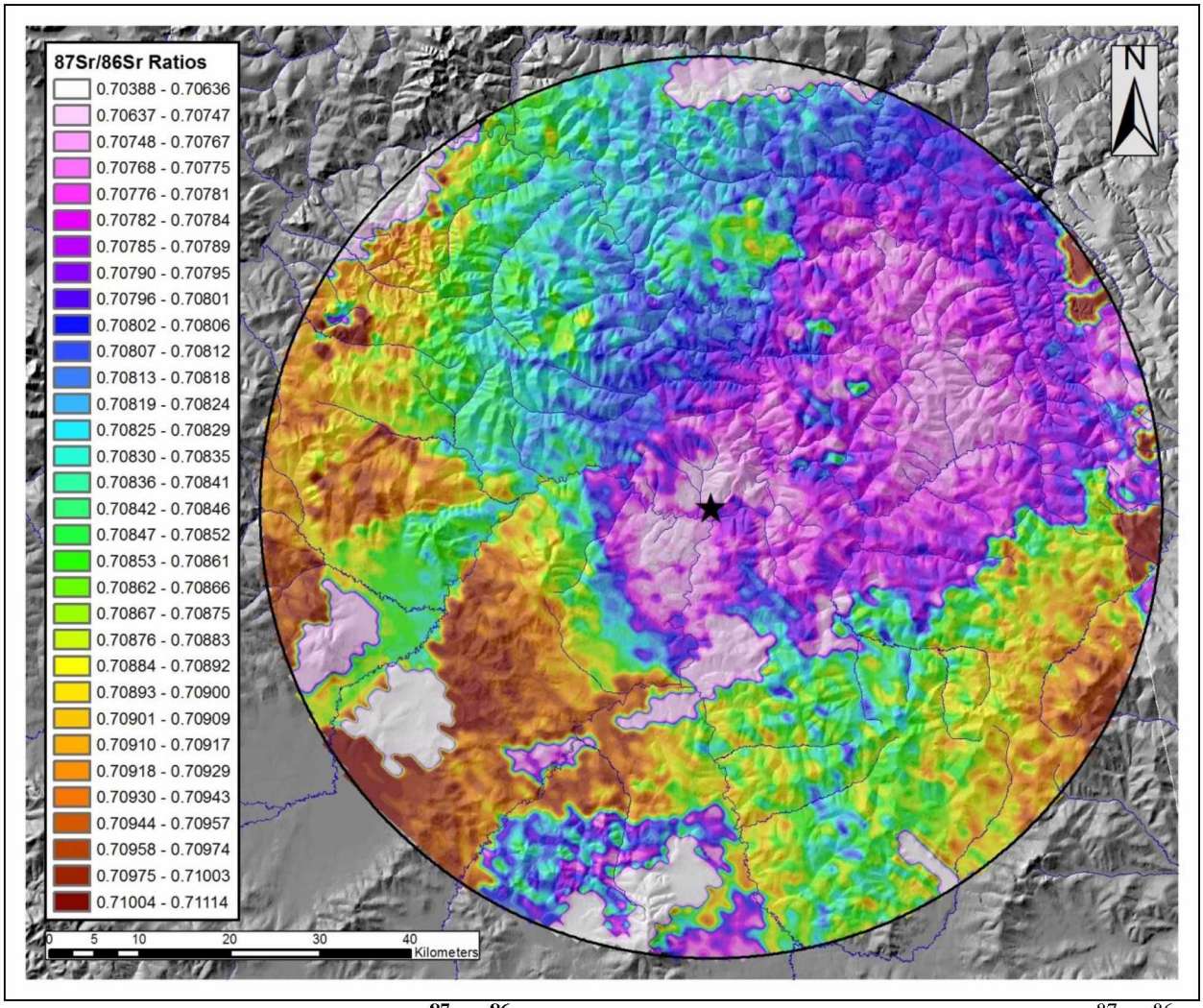

Figure 10. Lost Chicken Creek $^{87}Sr/^{86}Sr$ Isoscape. This map shows the variation in $^{87}Sr/^{86}Sr$ values in a 50 km radius from the Lost Chicken Creek Locale (represented by the black star). Derived from the Bataille et al. (2014) raster dataset.

the stratigraphy or provenience of the skeletal materials was recorded, and the Lost Chicken Creek paleontological collection now represents a palimpsest of species that spans at least 40,000 years.

The stratigraphy at Lost Chicken Creek is nearly 40 m deep, and is composed of silts, gravels, and peat that were formed from colluvial, fluvial, and eolian sources (Porter 1988). Faunal materials have been found in multiple stratigraphic units at the site, including the bison teeth used in this study. Porter (1988) published an extensive study on the stratigraphy at Lost Chicken Creek, and divided it into nine distinct units composed of gravels, silts, paleosols, and tephras that are capped with a thick layer of frozen muck at the top (Figure 11). Two tephras provide relative dates for the formation, including the Sheep Creek tephra that is present in the upper portion of the Unit 2 and has been dated via thermoluminescence to between 110,000 and 120,000 BP (Berger et al. 1996). This tephra is associated with *Equus lambei, Rangifer tarandus, Symbos cavifrons, Bison priscus*, and *Mammuthus primigenius* remains, but faunal materials are found throughout the deposits (Porter 1988). There is an inferred unconformity in Unit 3 as paleosols in the upper portion of the silts date to 9,560 ± 80 BP (Porter 1988), while the base of the unit is associated with the Sheep Creek tephra. The White River tephra is found near the surface of Unit 9, and dates to 1,700 ± 200 BP (Clague et al. 1995), providing a capping date to the formation (Porter 1988).

Unfortunately, provenience was not documented when the faunal materials from Lost Chicken Creek were collected. Therefore, there is no way to know which faunal materials are associated with which stratigraphic units, including the materials used in this study. All of the faunal materials at the locale were likely deposited by alluvial sources, although there is a possibility some of the faunal materials could have been transported by colluvial or solifluction

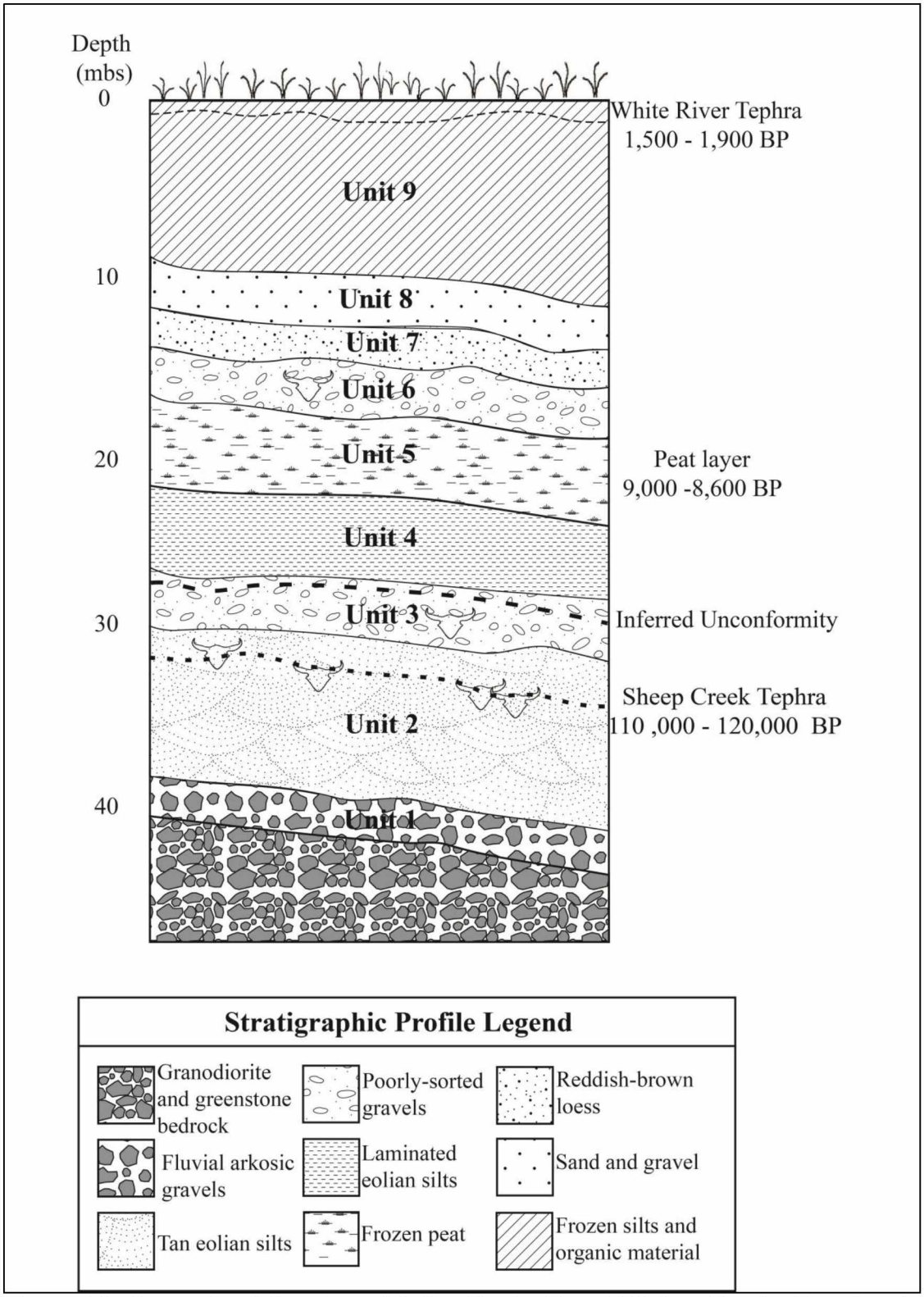

Figure 11. Generalized Stratigraphic Profile for Lost Chicken Creek. Based on information from Porter (1988).

(e.g., Thorson and Guthrie 1992) or by glacial advance during MIS4 (see Figure 3 for glaciation in the YTU). If the faunal remains were deposited from either glacial or alluvial processes however, they would have been from upstream locations. Lost Chicken Creek is not a large tributary, and has a relatively low hydrological volume, suggesting that the faunal materials would have been incorporated into the formation from nearby locations. This study assumes that the steppe bison teeth analyzed from this locale would have been deposited from within a relatively small radius of the Lost Chicken Creek.

5.2.3 Delta Region

This study also incorporates a control study to determine the reliability of the methods for interior Alaska. Information relating to the site locale and predicted $^{87}Sr/^{86}Sr$ and $\delta^{18}O$ values for this region are all discussed in a separate chapter (Chapter 6). However, the modern samples were collected and processed using the same methods and analyzed in the same facilities as discussed in this chapter.

5.3 AMS Radiocarbon Dating of Dental Collagen

All of the specimens from Lost Chicken Creek were submitted for AMS radiocarbon dating at the Center for Applied Isotope Studies (CAIS) at the University of Georgia, Athens. The specimen from the CRREL Permafrost Tunnel had been previously dated to 14,280 ±250 rcyBP (Canadian Archaeological Radiocarbon Database 2005). For the Lost Chicken Creek specimens, a section of dentine weighing ~4-5 g was removed from the root of each tooth using a using a handheld Dremel® with a diamond coated rotary wheel bit and then submitted for chemical processing and analysis at CAIS. The dentine samples were treated by a modified

Longin method using a sodium hydroxide extraction for humic substances and then combusted at 575°C. The recovered CO_2 was then cryogenically purified and converted to graphite on an iron catalyst at 580°C. AMS measurement was performed using National Electrostatics Corporation (NEC) model 1.5SDH-1 Pelletron accelerator with a reported error of under 0.1‰ (Cherkinsky et al. 2015). The results were corrected for isotopic fractionation and presented as radiocarbon years before 1950 (rcyBP) at one standard deviation, using a ^{14}C half-life of 5,568 years. The resulting radiocarbon dates were then normalized to represent years before present (cal. BP) using CALIB 7.0.2 software and the IntCal13 calibration curve (Reimer et al. 2013) and are presented in Table 2.

Collectively, the steppe bison teeth analyzed in this study represent a span of approximately 35,000 years. Only two of the specimens, UAMES-6616 and UAMES-6785, overlap at one standard deviation. Specimen UAMES-6335 was the youngest at ~15,290 BP, and represents the Late Pleistocene when climates were beginning to ameliorate (e.g., Cronin 1999). Specimens CRREL-FPT, UAMES-6173, and UAMES-6768, were calibrated to between 15,200 and 23,000 BP. The earlier part of this period is associated with the LGM, and climates would have been much cooler and dryer than at present (e.g., Elias and Brigham-Grette 2013). Specimens UAMES-6377, UAMES-6602, UAMES-6620, UAMES-6616, and UAMES-6785 were calibrated to between 31,400 and 38,500 BP. This period was a relatively warm interstadial period (MIS3) and forests reached nearly the same distribution as during the Holocene (e.g., Anderson and Lozhkin 2001). Specimens UAMES-12224, UAMES-6382, UAMES-8582, and UAMES-6594 date from approximately 38,500 calibrated years BP to ~47,500 radiocarbon years BP[5]. Climates during this time were transitioning from a relatively cool period, and would have

[5] AMS radiocarbon dates older than ~40,000 years BP cannot be calibrated with accuracy.

been much drier than during the warmer MIS3 interstadial (e.g., Anderson and Lozhkin 2001). Specimen UAMES-6599 dates to >51,550 radiocarbon years BP, and cannot be calibrated. Because of this, this specimen is not included in any temporal comparisons, but the $^{87}Sr/^{86}Sr$ results are still discussed in regards to reconstructing movement patterns and physical locations on the landscape.

Table 2. AMS Radiocarbon Dates for the Prehistoric Specimens. Radiocarbon error estimates signify one standard deviation (1σ) of the AMS date. The calibrated age range represents one standard deviation of the radiocarbon age.

Lab ID	Specimen ID	Locale	Radiocarbon Years BP	Calibrated Years BP
I-2197	CRREL-FPT	Fox Permafrost Tunnel	14,280 ±230	17,060-17,680
UGa-18101	UAMES-6335	Lost Chicken Creek	12,840 ±30	15,210-15,360
UGa-16694	UAMES-6173	Lost Chicken Creek	17,360 ±50	20,830-21,040
UGa-16699	UAMES-6768	Lost Chicken Creek	18,940 ±50	22,690-22,920
UGa-16695	UAMES-6377	Lost Chicken Creek	27,950 ±90	31,470-31,760
UGa-16696	UAMES-6602	Lost Chicken Creek	29,390 ±100	33,520-33,750
UGa-16698	UAMES-6620	Lost Chicken Creek	30,810 ±110	34,600-34,860
UGa-16697	UAMES-6616	Lost Chicken Creek	33,420 ±130	37,550-38,200
UGa-18105	UAMES-6785	Lost Chicken Creek	33,720 ±120	38,080-38,470
UGa-16701	UAMES-12224	Lost Chicken Creek	34,070 ±140	38,430-38,720
UGa-18102	UAMES-6382	Lost Chicken Creek	41,400 ±220	44,620-45,100
UGa-16700	UAMES-8582	Lost Chicken Creek	43,370 ±300	46,120-46,860
UGa-18103	UAMES-6594	Lost Chicken Creek	47,290 ±500	Invalid for calibration curve
UGa-18105	UAMES-6599	Lost Chicken Creek	>51,550	Invalid for calibration curve

This dataset encompasses a greater temporal period than many archaeological studies do. However, it is unique in that it covers several different climate phases and demonstrates change over a long span of time. Bison seasonal mobility has been reconstructed in several studies using

similar methods of time-series isotope sampling on dental enamel; however, all of the studies have analyzed specimens from a much more constrained temporal period of a few hundred to a few thousand years (e.g., Graves 2010; Julien et al. 2012; Widga 2006). Having a tight chronological control (i.e., samples overlapping at two standard deviations) is beneficial because they can then be treated as a population. However, analyzing samples from a constrained temporal period only demonstrates behavioral ecology for a short window of time. Studies have indicated that bison migration patterns can vary based on environmental factors (e.g., Grogan et al. 2010; Plumb et al. 2014), but to date, there have been no studies that have addressed steppe bison mobility patterns over multiple climatic periods. The wide temporal span of the samples used in this study is unique in that it addresses migration patterns during both glacial (MIS2) and interglacial (MIS3) periods, and has the potential for associating environmental change with behavioral changes.

5.4 Laboratory Methods

Serial-sampling tooth enamel for stable isotope analysis is a well-established method for observing change over time within a single individual, and has been applied to many studies addressing paleoecology and migratory behavior in ungulates including European steppe-bison (Julien et al. 2012), bison on the American Great Plains (Gadbury et al. 2000; Graves 2010; Widga 2006), Pleistocene horse and bison from the Sonoran Desert (Higgins and MacFadden 2004), Pleistocene caribou and bison from France (Britton et al. 2011; Bernard et al. 2009), and modern caribou from the Alaskan North Slope (Britton et al. 2009). Using serial-sampling methods, 132 individual samples from 17 prehistoric and modern bison teeth were collected using the following techniques.

5.4.1 Sampling for Time-Series Isotopic Analysis

The serial-sampling techniques followed standard methods of sampling and preparation for time-series isotopic analysis as reported in Britton et al. (2011), Higgins and MacFadden (2004), Widga et al. (2010), and others. After the teeth had been identified as *Bison priscus* (for prehistoric samples – the modern samples were from *B. b. bison*) and determined to be suitable for sampling they were cleaned with dental picks, a sterile toothbrush, and deionized water in the UAF Environmental Archaeology Lab. The surface portion of each tooth that was to be sampled was abraded with a steel carbide bit using a handheld Dremel® to remove approximately 0.1 to 0.2 mm of surface enamel that may have held particulate matter or contamination. After being cleaned, each tooth was marked in 4 mm increments beginning at approximately 2-3 mm above the cementoenamel junction (CEJ) of the tooth. Samples of enamel were collected by drilling out a 2-3 mm transect on the transverse plane of each tooth with 1 mm diamond-coated bit using a handheld Dremel® under the fumehood in the UAF Environmental Archaeology Lab.

After each sample was removed and collected, compressed air was used to clean the tooth and Dremel® of any particulate matter, and the drill bit was washed with detergent, rinsed with deionized water, and completely dried. Between 45-70 mg of powdered enamel was drilled out and collected in microcentrofuge tubes for each sample. The number of samples removed from each tooth depended on how worn the tooth was; an average 7-8 samples was removed from each tooth. The samples were then labeled sequentially, starting at Sample-1 for the first sample removed, Sample-2 for the second sample removed, and so on. Because teeth form from the top down, Sample-1 was always collected at the top of the tooth, nearest the occlusal surface, as it would represent the oldest portion of enamel (see Figure 12).

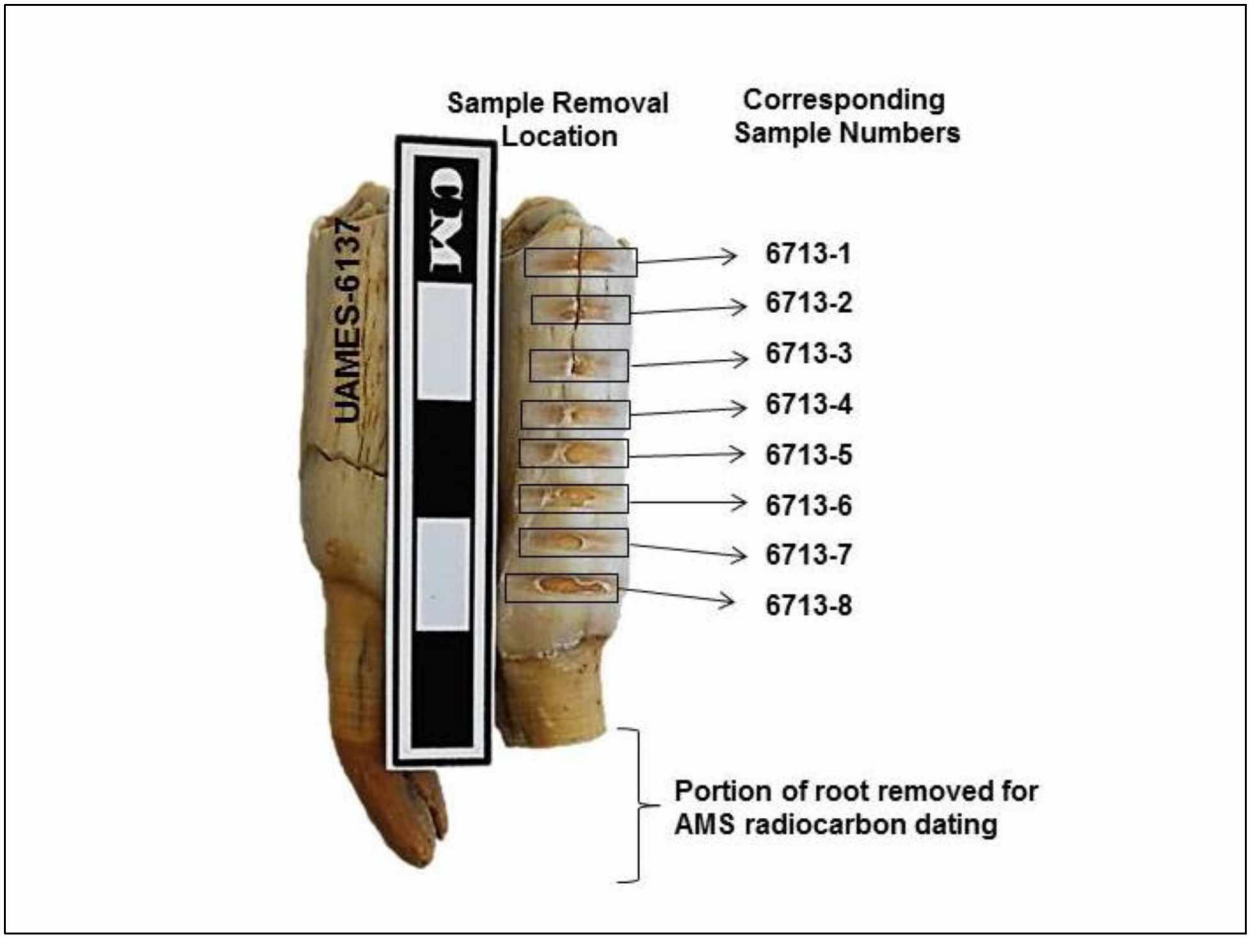

Figure 12. Example of Sample Placement. This shows specimen UAMES-6173 (*Bison priscus,* M_2) after sampling was complete. Eight samples, approximately 4 mm apart, were drilled out and collected. While the tooth is slightly worn down, sample 6713-1 represents the enamel that would have formed first (during the first summer of life). Sample 6713-8 represents enamel that would have formed last (during the first winter of life).

5.4.2 Chemical Preparation for $\delta^{18}O$ and $\delta^{13}C$ Analysis

After the samples were drilled out and removed, 25mg of powdered enamel was split off and prepared for $\delta^{18}O$ and $\delta^{13}C$ analysis in the UAF Chemical Archaeology Laboratory, following the methods outlined in Koch et al. (1997) and Widga et al. (2010). One milliliter of 2% sodium hypochlorite (NaOCl) was added to the samples and shaken to mix. The samples were left for 24 hours to remove organic particulates, and then centrifuged for 60 seconds on an

Eppendorf MinSpin plus centrifuge and rinsed three times with deionized water (centrifuging for 60 seconds between rinses). After the samples had been oxidized with NaOCl and rinsed, one milliliter of 1% acetic acid (CH_3CO_2H) was added to the samples and shaken to mix. The samples were left for four hours to purify the carbonate portion, and then centrifuged for 60 seconds and rinsed three times with deionized water (centrifuging for 60 seconds between rinses). After the chemical processing was complete, the samples were frozen for 8 hours and then freeze-dried for approximately 10 hours on a VirTiS benchtop Lyo-Centre lyophilizer.

5.4.3 Oxygen and Carbon Stable Isotope Analysis

Upon completion of the chemical processing, between 3-4 mg of each sample was weighed out on an Ohaus Adventure Pro microbalance for $\delta^{18}O$ and $\delta^{13}C$ analysis at the Alaska Stable Isotope Facility at the Water and Environmental Research Center at the University of Alaska, Fairbanks. Stable isotope data was obtained using continuous-flow isotope ratio mass spectrometry (CFIRMS). The samples were analyzed on a Thermo Scientific GasBench II carbonate analyzer coupled with a DeltaV Isotope Ratio Mass Spectrometer. CO_2 was separated chromatographically from other gases present in the samples and then transferred to the IRMS, where the oxygen and carbon stable isotopes were measured. Ten injections were performed for each sample, and the average and standard deviation of the ten injections was then calculated and reported. A blank sample was analyzed every twenty samples, and a laboratory standard (calcium carbonate) was analyzed every ten samples. NIST and IAEA standards were analyzed at the beginning of the sequence for calibration. The $\delta^{18}O$ values were reported relative to Vienna Mean Standard Ocean Water (V-SMOW) with a mean reported standard deviation of

0.26‰. The $\delta^{13}C$ values were reported relative to Vienna Pee Dee Belemnite (V-PDB) with a mean reported standard deviation of 0.33‰.

5.4.4 Strontium Isotope Analysis

After sampling was complete, 20 mg of each individual sample was split off and sent to the Strontium Isotope Geochemistry Laboratory at the University of Utah, Salt Lake, to be chemically prepared and analyzed for $^{86}Sr/^{87}Sr$ on a Thermo Scientific, High Resolution Neptune (Bremen, Germany) Multicollector-Inductively Coupled Plasma Mass Spectrometer (MC-ICPMS). The University of Utah laboratory used a method which was developed there to purify Sr for the $^{86}Sr/^{87}Sr$ analysis via an introduction system of aqueous solution using an inline chromatographic column (see Brennan et al. 2014 and Mackey and Fernandez 2011 for additional information on the purification process). Blanks or standard reference material SRM987 (National Institute of Standards and Technology 2014) was run between samples. Duplicate analysis was run on several samples (n=13), with a resulting precision of ±0.00002. The mean reported standard error was 0.00001 for all samples.

5.5 Summary

Both the modern and prehistoric samples used in this study are associated with the YTU and Tanana Basin region in interior Alaska, and were sampled and prepared for isotope analysis using standard methods. Isoscapes from Bataille et al. (2014) and Sloat (2014) have provided expected distribution of $^{87}Sr/^{86}Sr$ and $\delta^{18}O$ values for the study region, and will be used to contextualize the results discussed in Chapter 7. AMS radiocarbon dates have provided temporal context for the samples, and demonstrate that the prehistoric teeth encompass the most recent

stadial and interstadial periods, indicating that there may be potential to associate different migration patterns (if there are any) with different climatic periods. However, these time-series isotopic methods have never been applied to prehistoric studies in Alaska, and there are potential issues with identifying mobility based on $^{87}Sr/^{86}Sr$ variation in permafrost regions (i.e., Douglas et al. 2013). Therefore, this study also incorporated a control study using modern samples from the Delta Bison Herd (applying the same methods as the prehistoric samples) to determine if $^{87}Sr/^{86}Sr$ and $\delta^{18}O$ values would be a valid way to reconstruct prehistoric bison behavioral ecology in the Tanana Basin region. The history, behavioral ecology, and known seasonal patterns, as well as the results and implications of this control study are discussed in the next chapter.

CHAPTER 6: MODERN CONTROL STUDY

As discussed in previous chapters, reconstructing the behavioral ecology of prehistoric species can be challenging, and there are many factors associated with mineralization processes and the bioaccumulation of isotopic signatures that are not fully understood. Additionally, there have been relatively few studies that have used $^{87}Sr/^{86}Sr$ to reconstruct animal mobility patterns in circumpolar regions, and a study by Douglas et al. (2013) has indicated that $^{87}Sr/^{86}Sr$ signatures may vary in riverine systems due to the freeze-that cycle, which has the potential to obscure migratory signatures for organisms consuming water from those systems. This study also incorporates the newly-modeled $^{87}Sr/^{86}Sr$ isoscape that Bataille et al. (2014) published, and unfortunately, the isoscape did not predict the variation of YTU as accurately as other regions in the state (see Section 5.1). Each of these factors has the potential to confound the reconstruction of steppe bison behavioral ecology. Therefore, a modern control study was conducted to determine how well the isoscape (Bataille et al. 2014) predicted the variability in the Tanana Basin/YTU region, and whether there were issues with tracking known migratory patterns of bison with $^{87}Sr/^{86}Sr$ and $\delta^{18}O$ isotopic signatures. The specimens were from the Delta Bison Herd near Delta junction, which was transplanted there in the 1920s and is managed by the Alaska Department of Fish & Game (ADF&G).

6.1 Use of Modern Samples as a Control

The main objective of this study is to explore steppe bison behavioral ecology, especially focusing on seasonal migration and mobility. This will be accomplished by measuring and analyzing strontium and oxygen isotopes from sequentially-sampled bison teeth. The same method has been applied to several other studies addressing paleo-bison mobility (e.g., Britton et

al. 2011; Julien et al. 2012; Graves 2010; Widga 2006) as well as mobility patterns of other ungulate species (e.g., Balasse et al. 2003; Bendry et al. 2009; Britton et al. 2009). As discussed in Chapter 4, measuring $^{87}Sr/^{86}Sr$ values in skeletal materials is an especially well-suited for exploring geographical affiliation in biological organisms because the ratios have regional variability. However this method has had limited application in Alaska, and to date, there are only two studies that have used $^{87}Sr/^{86}Sr$ values to explore mobility patterns. This may in part be due to the fact that a state-wide isoscape for $^{87}Sr/^{86}Sr$ variation was only recently published (i.e., Bataille et al. 2014).

The first study was conducted by Britton et al. (2009) and used both strontium and oxygen isotopes to reconstruct seasonal migration in modern caribou herds on the North Slope. Part of the study goal was to determine if strontium and oxygen isotopes were a valid way to track migration in northern regions; the results tracked very well with the known migratory patterns of the herd and suggested that this could have applications for paleostudies (Britton et al. 2009). A second study was conducted by Brennan (2014) and sought to track salmon migratory behavior and determine their spawning locations in the Nushagak watershed in northwest Alaska. The results demonstrated that by measuring the $^{87}Sr/^{86}Sr$ values in salmon otoliths, the fish could be tracked to small tributaries and sub-basins which has important implications for managing fisheries in Bristol Bay (Brennan 2014). As part of this research, Brennan et al. (2014) also developed a high-resolution hydrological isoscape for $^{87}Sr/^{86}Sr$ distribution in Alaskan watersheds. Now that a terrestrial isoscape (Bataille et al. 2014) and hydrological characterization (Brennan et al. 2014) for $^{87}Sr/^{86}Sr$ values has been developed for the entire state of Alaska, it is likely that strontium isotopes will be used more frequently to reconstruct the movement patterns of both modern and prehistoric species.

Unfortunately, there is an issue in permafrost regions which may confound studies seeking to reconstruct seasonal mobility patterns from $^{87}Sr/^{86}Sr$. A study conducted by Douglas et al. (2013) in the Chena River in the YTU indicated that there is seasonal variation in $^{87}Sr/^{86}Sr$ ratios due to the freeze/thaw cycle, which changes the depth and location of hydrological output between summer and winter seasons. Ratios of $^{87}Sr/^{86}Sr$ in riverine systems are a reflection of water catchment from upstream locations (e.g., Aubert et al. 2002), but this factor is dependent on flow rates and the depth of the water table. Summer catchment will contain a greater proportion of surficial water sources, but winter catchment (especially for northern regions) will have less surficial contribution and will often be derived from deeper bedrock sources, thus creating fluctuations in the $^{87}Sr/^{86}Sr$ sources. These factors are also dependent on variation in precipitation and temperature which alters the hydrological input. These factors all contributed to $^{87}Sr/^{86}Sr$ ratios in the Chena River to shifting as much as 0.0050 of the course of a year; the lowest measured $^{87}Sr/^{86}Sr$ ratio was 0.7212 in January and highest measured $^{87}Sr/^{86}Sr$ ratio was 0.7262 in July (Douglas et al. 2013). Strontium variability is considered significant in the fifth decimal (i.e., Bentley 2006), suggesting that this seasonal variation in the hydrological cycle is particularly problematic for applications of $^{87}Sr/^{86}Sr$ in high latitude regions. Furthermore, there is no way to determine how this process functioned in the past, and considering the many variations in climate over the past 50,000 years, $^{87}Sr/^{86}Sr$ in hydrological systems almost certainly would have fluctuated.

While this initially seems problematic for reconstructing prehistoric mobility patterns, there are two reasons why this may not be a significant issue for reconstructing steppe bison behavioral ecology. First, the work by Britton et al. (2009) demonstrated that $^{87}Sr/^{86}Sr$ values in caribou tracked very well with known seasonal migration patterns, and there was no indication

that seasonal hydrological fluctuations affected the migratory signature of the specimens. Second, ungulates derive a majority (45% ±15) of their bodily water from food sources for $\delta^{18}O$ (Kohn and Cerling 2002), suggesting that similar proportions of $^{87}Sr/^{86}Sr$ would be derived from diet as well (however, this relationship has yet to be quantified in the literature for $^{87}Sr/^{86}Sr$). Therefore, while the seasonal ratios of $^{87}Sr/^{86}Sr$ in drinking sources may have fluctuated in the past, this would have only contributed to a portion of the $^{87}Sr/^{86}Sr$ ratios in steppe bison dental enamel, and only then if they were consuming all of their drinking water from larger riverine systems. While seasonal fluctuation of $^{87}Sr/^{86}Sr$ could have contributed to the signatures of the prehistoric specimens, the input is assumed to be minimal and likely would not have obscured any actual migratory signatures.

However, in response to the limited number of migratory studies for permafrost regions, the potential issues with hydrologically-derived $^{87}Sr/^{86}Sr$ seasonal variation, and the issues with the Bataille et al. (2014) model accurately predicting the variation for the YTU (see Section 5.1), this study incorporated a control study analyzing $^{87}Sr/^{86}Sr$, $\delta^{18}O$, and $\delta^{13}C$ from sequentially-sampled modern bison (*B. b. bison*) teeth from the Delta Bison Herd applying the same methods as were used for the prehistoric samples. This control study focuses on three primary questions: 1) how well does the strontium isoscape published by Bataille et al. (2014) match the $^{87}Sr/^{86}Sr$ results in the Delta region; 2) does the seasonal variation of $^{87}Sr/^{86}Sr$ and $\delta^{18}O$ match the known migratory patterns of the herd; and 3) how reliable are the methods in this study for reconstructing prehistoric seasonal mobility patterns in the Tanana Basin and YTU, and permafrost regions in general.

6.2 History of the Delta Bison Herd

There are no naturally occurring bison species in Alaska today, but in 1928 a herd of 17 plains bison (*B. b. bison*) from the National Bison Range in Montana were introduced to the Delta Junction Region, about 150 km southeast of Fairbanks, Alaska. The bison were imported due to a somewhat misguided interest in establishing Alaska as a game-hunter's paradise, and represented one of many early attempts at (re)introducing animals to the territory (Coates 1997). The Delta region was chosen because unique climate patterns in the early 1920s allowed large grassy meadows to spread out along the confluence of the Delta and Tanana Rivers which were apparently nutritious enough to support the over-wintering of small herds of horses and mules that local prospectors would release to fend for themselves until the following summer (Coates 1997). The meadows unfortunately did not remain established, but nevertheless, the bison adapted well to the riverine and upland ecotones along the Tanana and Delta River, and by the 1940s had reached some 500 individuals and could support some sport hunting as well as the establishment of herds in other regions (Coates 1997; Gipson and McKendrick 1981; Paul 2009). In 1950, the U.S. Fish and Wildlife Service transplanted 17 individuals to the Copper River Valley and in 1962, ADF&G (managers of the herd since statehood in 1959) transplanted 39 more bison to the Chitna River area in hopes of bolstering the Copper River herd (Paul 2009). Finally, between 1965 and 1968, a total of 38 individuals were transplanted to the Farewell Lake region in northwest Alaska (Paul 2009).

The Delta Bison Herd remains a healthy and viable population, but is heavily managed by ADF&G. It is the largest out of the four plains bison herds in Alaska, numbering about 450-500 individuals depending on season and hunting activities (Alaska Department of Fish & Game 2015). The Copper, Chitna, and Farewell herds are smaller, only numbering around a hundred

individuals per herd (Paul 2009). The Alaskan herds represent some the few (or only) plains bison herds that do not have genetic admixture from domesticated cattle (Paul 2009). Nevertheless, the behavioral ecology of the herds, especially the Delta Herd, is heavily influenced and manipulated by human activity (i.e., Gipson and McKendrick 1981; Paul 2009), and therefore cannot be considered a reliable proxy for modeling diet and migration choices for prehistoric bison. However, the same physiological and geologic processes are still at work for this herd and the region which they inhabit, and for that reason provide an excellent proxy for assessing and identifying issues with reconstructing mobility patterns from strontium and oxygen isotope ratios.

6.3 Seasonal Mobility and Diet Patterns

The Delta Herd is closely monitored by ADF&G, and because of this, the seasonal migration patterns and dietary preferences are well known. The bison migrate between different ecotones on a seasonal basis, averaging a total distance of ~150 km throughout the year within a ~50 km radius. Wildlife biologist and bison specialist Darren Bruning (personal communication, 2014) described the seasonal migratory patterns of the herd as follows (see Figure 13 for a map of the seasonal ranges):

The winter range is the largest, and a majority of the herd spends the winter in the region east of Jarvis Creek, west of the Gerstle River, north of the Granite Range, and south of the Tanana River. The outlet of Healy Lake and the boggy areas near the headwaters of the Delta Clearwater River are favored regions, and this may relate to the availability of open water sources during the winter. Some individuals range across the Alaska Highway during the winter as well.

In April the herd begins to moves south, following the Gerstle River upstream and crossing the Alaska Highway before traveling west along the lower contours of the Granite Range to reach the spring calving grounds along Granite Creek and to the north of Donnelly Dome. This is where the calves are born each May, and while the majority of births occur near Donnelly Dome, some have been observed as far north as Jarvis Creek, and as far south as the Black Rapids Glacier.

During summer the herd is dispersed throughout the Delta River basin, favoring gravel bars, vegetated outwash plains, and old glacial terraces along the river banks. Their distribution is from approximately 8 miles north of Donnelly Dome, throughout the Delta River basin to Black Rapids Creek in the south. During June and July the herd is mostly dispersed. Within the past decade, portions of the herd have been observed several miles west of the Delta River on upland terraces near Delta Creek. Bruning (personal communication, 2014) reported that there were relatively small differences in the migratory behavior between sexes, but he did note that solitary bulls have been observed in the Delta River/Jarvis Creek floodplain during the summer, and in the Gerstle River floodplain in late summer and early fall, and bulls have been observed in higher elevation areas than cows.

Beginning in August, the herd migrates to the area between Jarvis Creek and Gerstle River for the fall rut. Bruning (personal communication, 2014) reported that the herd displays high fidelity to this mating area and the herd congregates there for about a month. Late fall and winter ranges are nearly identical, but the fall range incorporates higher elevation areas along the northern foothills of the Granite Range, while winter incorporates lower elevation foothills north of the range.

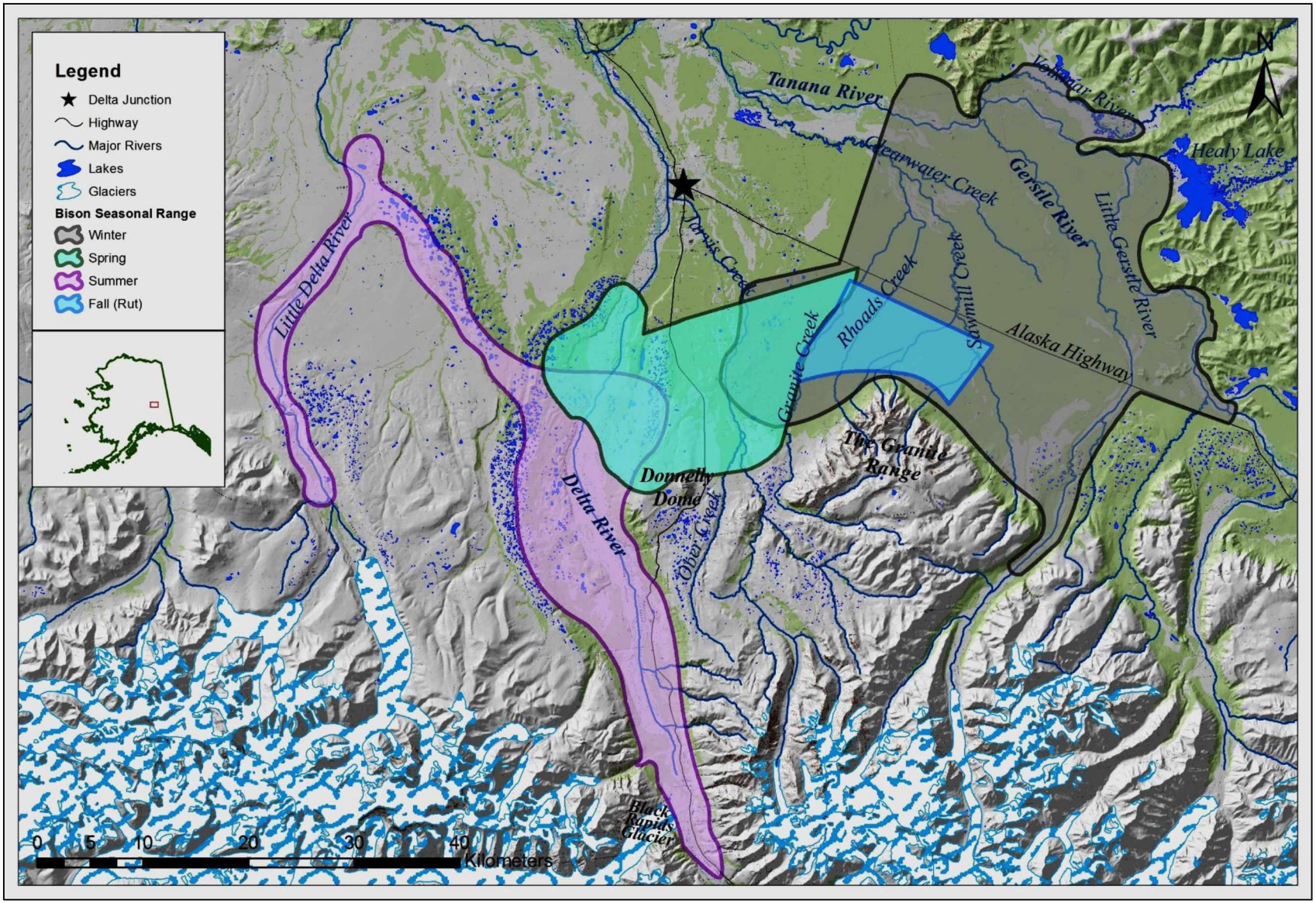

Figure 13. Seasonal Ranges for the Delta Bison Herd. Fall and winter ranges for the herd are nearly identical, with the exception of a few weeks in August when the herd congregates between Sawmill and Granite Creeks for mating season.

One major factor which affects the behavioral ecology of the Delta Herd is the presence of agricultural fields in the region. In the 1950s and 1960s several farms were homesteaded and agricultural fields were established along Jarvis and Clearwater Creeks which were habitat areas favored by the herd (Gipson and McKendrick 1981). During the 1970s even more fields were developed in the region when Alaska initiated a program to expand agriculture production for the state. Nearly 60,000 acres east of Delta Junction were developed as part of this initiative and most of the new fields were located in prime bison habitat (Coates 1997; Gipson and McKendrick 1981). Not only were the fields located in areas that the bison already used, but the crops also offered highly nutritious and appetizing food sources for the bison, especially in late August and September when the productivity of their summer range along the Delta River had begun to decline (Coates 1997).

As the bison began to cause damage to the yearly harvests through trampling and consuming crops, unhappy farmers put increasing pressure on ADF&G to find a solution, and in 1970s the Alaska legislature established the 90,000 acre Delta Junction Bison Range (DJBR) south of the Alaska Highway (Coates 1997). The primary goal of establishing the Range was to improve forage away from the agricultural fields so as to prevent the bison from migrating into those areas until after the fields had been harvested (Coates 1997). As of 2006, almost 3,000 acres on the DJBR had been cleared and selectively planted and was producing high volumes of nutritious forage (Dubois 2006). Other management tactics have included bulldozing corridors to funnel the bison into certain areas, controlled burning to reduce woody vegetation and establish herbaceous plants, and setting up salt licks to encourage the bison to stay away from agricultural fields (Coates 1997; Paul 2009). While the Delta Herd does migrate on a seasonal basis, these movement patterns are clearly structured by human intervention.

The diet of the Delta Bison Herd also does not reflect the actual natural availability of food sources in the Delta region. When not sneaking bites out of agricultural fields, or being fed imported foods, the bison typically consume herbaceous sedges, graminoids, and forbs, and occasionally incorporate browse into their diets. They especially favor vetch (*Vicia*) and silverberry (*Elaeagnus*) which grow in abundance on the gravel bars along the Delta River, as well as willow (*Salix*), and dwarf birch (*Betula nana*; Alaska Department of Fish & Game 2015).

6.4 Results and Discussion

Three teeth from two modern bison from the Delta Bison Herd were used in this comparative study. The teeth were collected by ADF&G and were from individuals that were harvested during 2012-2013. The sex of the individuals was not recorded, but based on dental wear both individuals were between 4-6 years of age. An M_2 and an M_3 from a single individual (DH1) was sampled, along with an M_3 from another individual (DH2), using the same methods as presented in Chapter 5. The resulting samples were analyzed for $^{87}Sr/^{86}Sr$, $\delta^{18}O$, and $\delta^{13}C$ at the same facilities and with the same reported standard error as presented in Chapter 5.

Based on the $^{87}Sr/^{86}Sr$ isoscape published by Bataille et al. (2014), the expected range of variation in a 50 km radius around the Delta region was between 0.7075 and 0.7429. The population $^{87}Sr/^{86}Sr$ mean was 0.71607 ±0.00043, which it within the expected range. The resulting $\delta^{18}O$ population mean was -19.3 ±1.0‰, which also fits expectations for $\delta^{18}O$ distribution (see Figure 7; Sloat 2014). However, the magnitude of the sinusoidal wave (difference between the highest summer and lowest winter values) for the $\delta^{18}O$ is less than expected for a high latitude region with marked seasonality. Other mid-latitude studies have reported a range of 4-5‰ for the magnitude of the $\delta^{18}O$ seasonal variation (Fricke and O'Neil

1996; Julien et al. 2012; Widga et al. 2010) but this dampened signal in the modern specimens may be related to seasonal elevation changes. Based on 1:63,360 USGS contour maps, the Delta Herd traverses an elevation gradient of over 1,000 ft. between seasons, inhabiting areas between 2,000-3,000 fasl in summer, and ~1,200 fasl in winter. This change in elevation would create a dampened $\delta^{18}O$ signal as there is an altitudinal gradient of $\delta^{18}O$ with higher elevation regions having relatively lower $\delta^{18}O$ signatures and lower elevation regions having relatively higher $\delta^{18}O$ signatures (Bowen et al. 2005; Sloat 2014). The $\delta^{13}C$ population mean was -14.7 ±0.3‰ which suggests a very homogenous diet throughout the year and is consistent with the consumption of C_3 plants. The $\delta^{13}C$ results are not discussed further in this chapter. The mean, standard deviation, range and amplitude for the $^{87}Sr/^{86}Sr$ and $\delta^{18}O$ values are presented in Table 3 (see Appendix A for all modern isotope values including $\delta^{13}C$).

Table 3. Summary $^{87}Sr/^{86}Sr$ and $\delta^{18}O$ Results for the Modern Delta Herd. The mean, standard deviation (SD), and range for $^{87}Sr/^{86}Sr$ is presented, along with amplitude (Amp.) for $\delta^{18}O$. Standard deviation is determined based on the specimen mean. Amplitude is determined as the difference between the highest and lowest value for that specimen.

Sample ID	# Samp. Removed	$^{87}Sr/^{86}Sr$			$\delta^{18}O$ (‰)			
		Mean	*SD*	*Range*	*Mean*	*SD*	*Range*	*Amp.*
DH1a	8	0.71583	0.00033	0.71523 to 0.71628	-18.7	1.2	-17.2 to -20.8	3.6
DH1b	8	0.71590	0.00035	0.71540 to 0.71635	-19.4	0.9	-18.6 to -20.8	2.7
DH2	11	0.71637	0.00038	0.71582 to 0.71714	-19.7	0.7	-18.5 to -20.6	2.1

6.4.1 How well does the strontium isoscape published by Bataille et al. (2014) perform?

Based on the dataset published by Bataille et al. (2014), and constraining the isoscape to a 50 km radius encompassing the known bison habitat, the expected range for the $^{87}Sr/^{86}Sr$ values

is between 0.7075 and 0.7429 (see Figure 14). However, the isoscape for the Delta region indicates that the majority of the $^{87}Sr/^{86}Sr$ range is between 0.7135-0.7199 and there are only a few localized regions with higher or lower values. This suggests that means for all three specimens should fall into this range with the actual measured $^{87}Sr/^{86}Sr$ means for the specimens representing a homogenization of those values. The $^{87}Sr/^{86}Sr$ mean for specimen DH1a is 0.7158

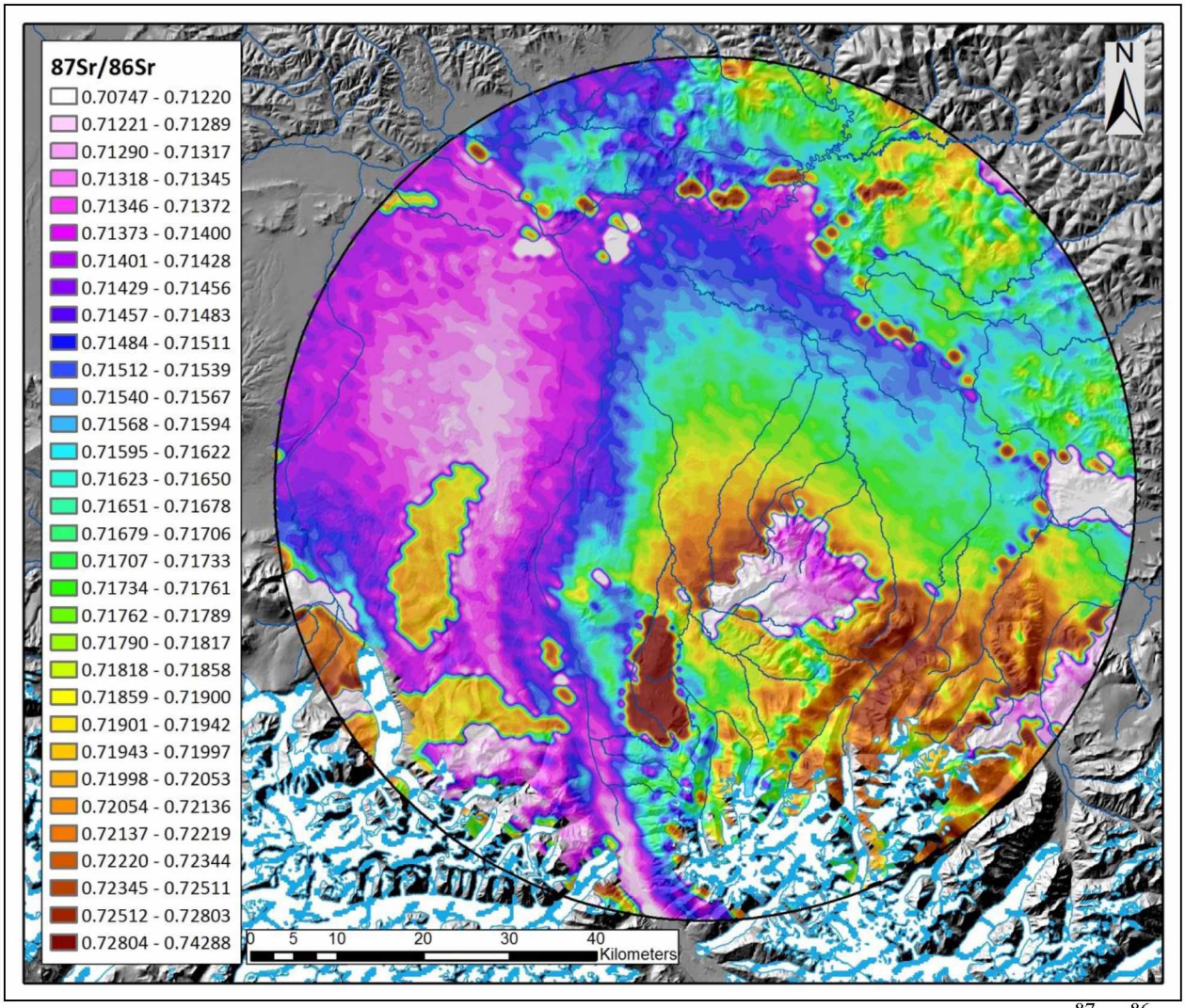

Figure 14. Strontium Isoscape for the Delta Herd Region. This map shows the $^{87}Sr/^{86}Sr$ variation for a 50 km radius around the Delta Bison Herd know habitat region. Derived from the Bataille et al. (2014) raster dataset.

the mean for DH1b is 0.7159, and the mean for DH2 is 0.7164. This suggests that the model (Bataille et al. 2014) performs extremely well for this region. Additional seasonal-specific analysis (discussed below) further demonstrates that the isoscape models the bioavailable $^{87}Sr/^{86}Sr$ values exceptionally well, with a strong correlation between the seasonal $^{87}Sr/^{86}Sr$ values and seasonal habitat areas favored by the bison. These results suggest that the predictive model developed by Bataille et al. (2014) is also representative of $^{87}Sr/^{86}Sr$ values for other regions of the Tanana Basin and YTU, including the region associated with the CRREL Permafrost Tunnel and the Lost Chicken Creek locality.

6.4.2 Does the seasonal variation of $\delta^{18}O$ and $^{87}Sr/^{86}Sr$ fit the known migratory patterns?

As discussed in Section 4.2, oxygen stable isotopes show seasonal variation in values due to summer/winter precipitation processes of the meteoric water cycle (Gat 1996). When graphed, the resulting $\delta^{18}O$ values will appear as a sinusoidal wave, varying between high values in the summer and low values in the winter (e.g., Fricke and O'Neil 1996). This is a well-established method for identifying seasonality, and has been used in many studies that have utilized serial-sampling techniques on dental enamel for reconstructing animal behavioral ecology on a seasonal basis (e.g., Bernard et al. 2009; Britton et al. 2011; Fricke et al. 1998; Higgens and MacFadden 2004; Julien et al. 2012;). The graph of $\delta^{18}O$ results for the modern samples demonstrates this sinusoidal pattern (Figure 15), and by comparing the $\delta^{18}O$ results to the $^{87}Sr/^{86}Sr$ values, season can be correlated with change in geographical location (Figure 16).

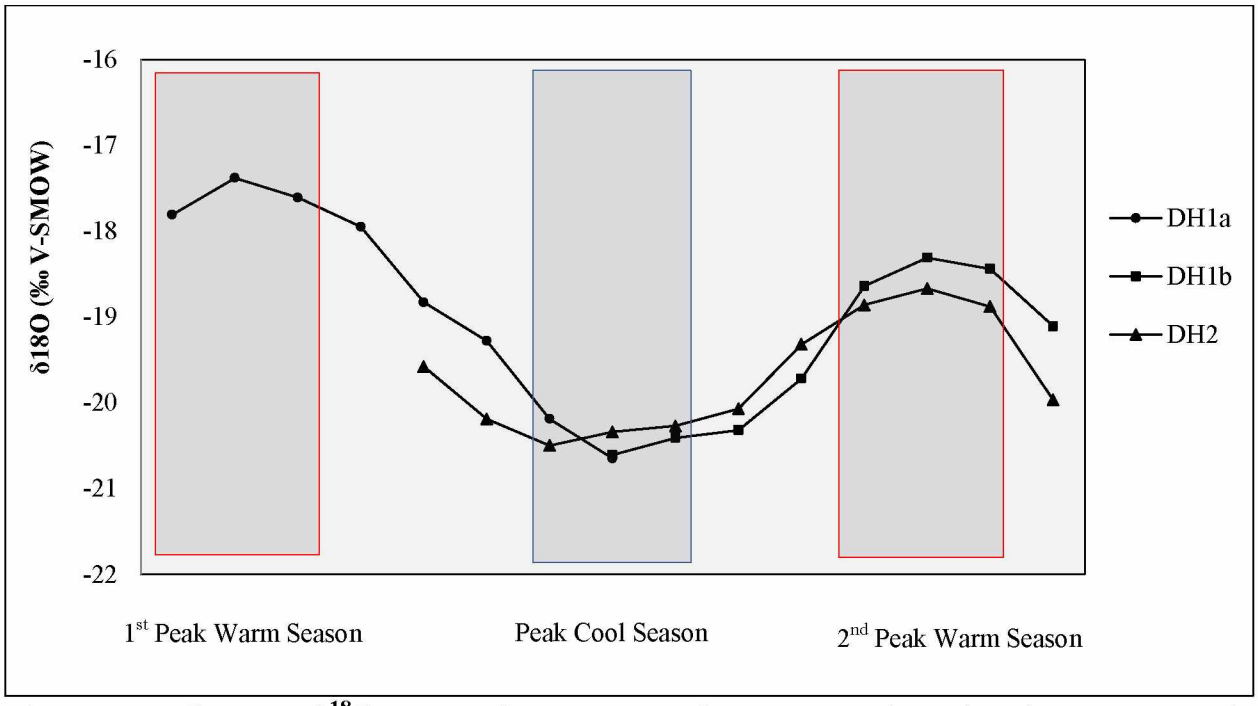

Figure 15. Graphed $\delta^{18}O$ Values for the Delta Samples. Peak cool and warm season is determined based on the peaks and troughs of the sinusoidal-wave pattern.

Because the Delta bison inhabit well-documented ranges on a seasonal basis, the variation in seasonal $^{87}Sr/^{86}Sr$ values can be further restricted (see Table 4 and Figure 17). The bison summer range has the lowest mean $^{87}Sr/^{86}Sr$, followed by the spring calving range. The area where the bison spend the fall rut has the highest mean $^{87}Sr/^{86}Sr$ values, followed by the winter range. In general, the expected pattern would be relatively low $^{87}Sr/^{86}Sr$ values before the peak warm season, with the $^{87}Sr/^{86}Sr$ values increasing after the peak warm season, and then decreasing slightly during the cool season. However, all of the ranges, with the exception of the fall range, have high SD, indicating that the actual $^{87}Sr/^{86}Sr$ values could vary from this pattern. Additionally, individual bison, such as the ones in this study, may have migratory behavior that deviates from the general pattern of the herd, and the seasonal ranges encompass all potential areas that bison might inhabit.

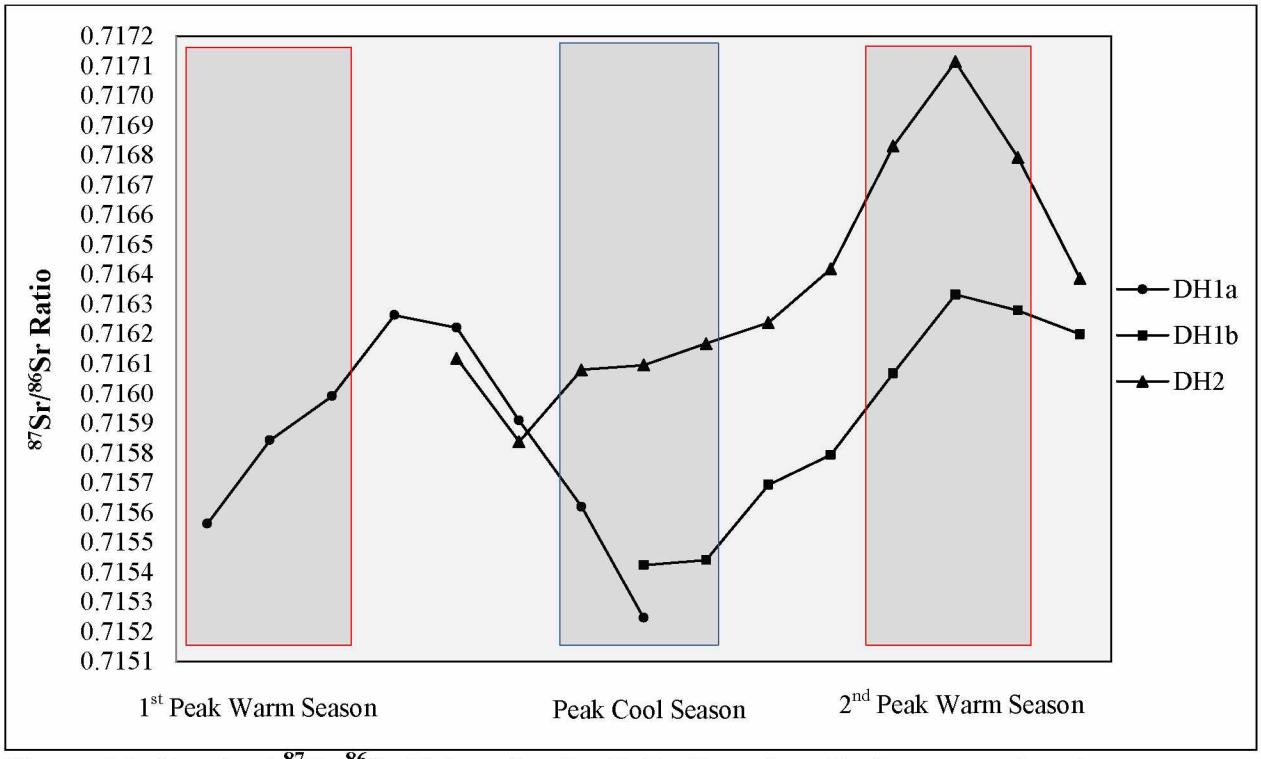

Figure 16. Graphed $^{87}Sr/^{86}Sr$ Values for the Delta Samples. Peak warm and cool seasons was determined based on comparison with Figure 15.

In general, the $^{87}Sr/^{86}Sr$ values echo the expected pattern, although there is a decrease in the measured ratios during the cool season which does not match the expected pattern of the means. This could be a result of these individual bison inhabiting a more contained region during the winter such as the boggy area between the Tanana and Delta Clearwater Rivers. Bruning (2014) noted that this region was a favored wintering spot for the herd, and they generally aggregate in this region in mid-winter. This region has lower $^{87}Sr/^{86}Sr$ values than the mean for the entire winter range (see Figure 17 for detailed maps of seasonal range $^{87}Sr/^{86}Sr$ variation), which would cause the bison to have the lower $^{87}Sr/^{86}Sr$ winter signature that is reflected in the data. Even with the decrease in the $^{87}Sr/^{86}Sr$ signatures during the cool season,

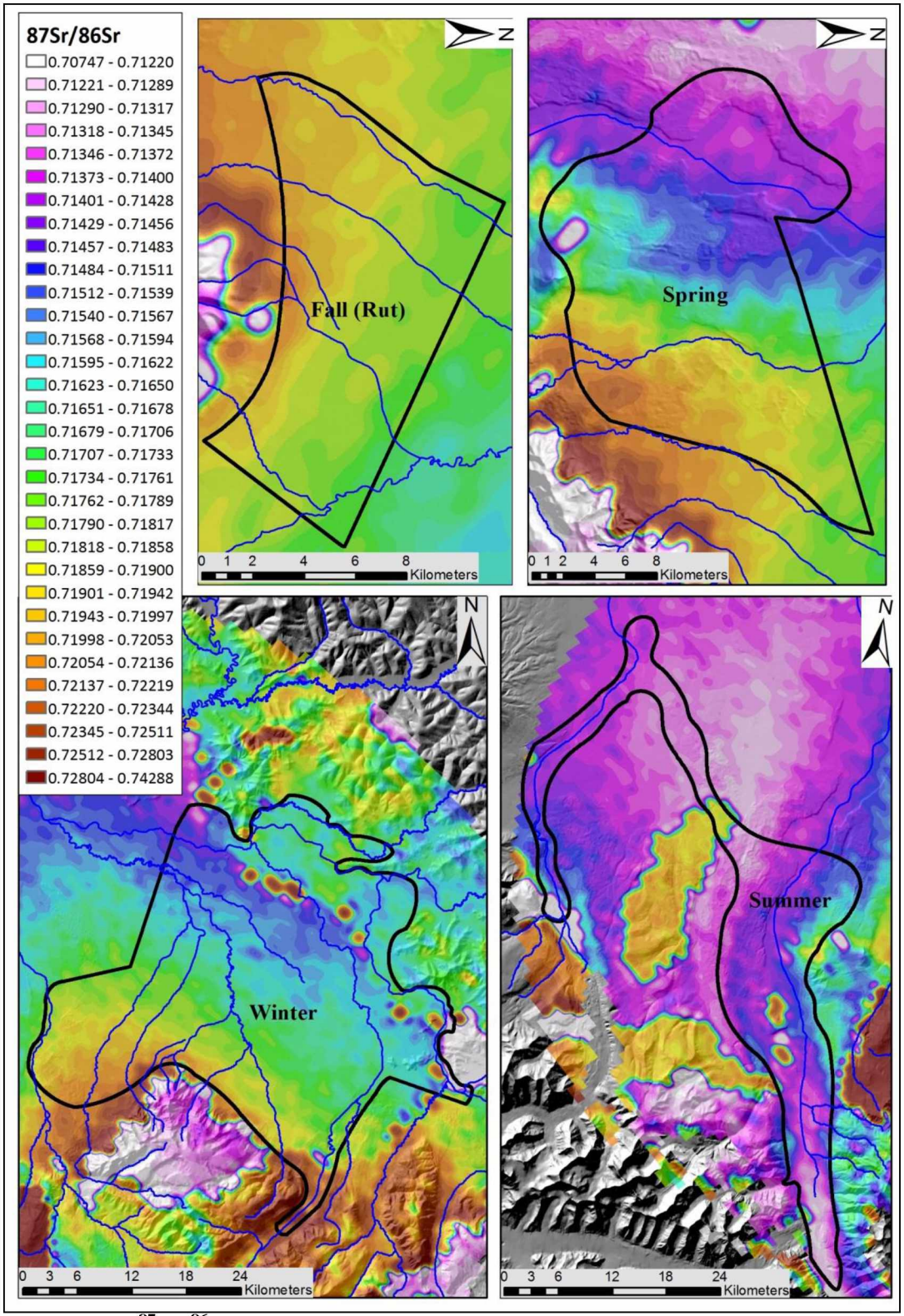

Figure 17. $^{87}Sr/^{86}Sr$ Variation for the Delta Herd Seasonal Ranges. Ranges from Bruning (personal communication, 2014) and the $^{87}Sr/^{86}Sr$ raster dataset is from Bataille et al. (2014)

the $\delta^{18}O$ and $^{87}Sr/^{86}Sr$ track remarkably well with known seasonal migration for the Delta Herd, and the $^{87}Sr/^{86}Sr$ seasonal signatures fall well within the SD for the seasonal ranges. The techniques used in this control study indicate that this is an appropriate for reconstructing prehistoric migratory behavior on a seasonal basis.

Table 4. Seasonal Habitat Mean $^{87}Sr/^{86}Sr$ and Variation. The seasonal habitat means were derived from the Bataille et al. (2014) raster dataset. This variation is illustrated in Figure 17.

Season	Mean	SD	Min	Max
Summer	0.71443	0.00153	0.7094	0.7239
Spring	0.71685	0.00236	0.7105	0.7234
Winter	0.71725	0.00205	0.7106	0.7313
Fall	0.71854	0.00090	0.7172	0.7217

6.4.3 How reliable are $^{87}Sr/^{86}Sr$ and $\delta^{18}O$ for reconstructing seasonal mobility patterns in the Tanana Basin and YTU, and permafrost regions in general?

Based on the results, $^{87}Sr/^{86}Sr$ and $\delta^{18}O$ values appear to be reliable tools for reconstructing bison mobility patterns on a seasonal basis. The $\delta^{18}O$ values show clear sinusoidal patterns for both of the specimens, varying between peak cool and warm seasons. Correlating the $\delta^{18}O$ values with the $^{87}Sr/^{86}Sr$ results demonstrated the seasonal range of $^{87}Sr/^{86}Sr$ values for the two modern bison. These results were similar to expected patterns of variation based on the means for the different habitat ranges (Bataille et al. 2014). From a methodological standpoint, serial-sampling bison teeth and correlating $^{87}Sr/^{86}Sr$ and $\delta^{18}O$ values is a reliable way to determine seasonality and changes in geographical location.

One factor that is demonstrated by this control study is that the input of $^{87}Sr/^{86}Sr$ during the mineralization process is complex, and represents a homogenization of values over several

weeks. This factor was expected based on a volume of research (Balasse 2002; Bentley 2006; Kohn and Cerling 2002; Zazzo et al. 2006 and others), but further demonstrates this relationship based on comparisons of the fine-scale $^{87}Sr/^{86}Sr$ distribution maps (Bataille et al. 2014). This control study additionally demonstrates that strontium isotope ratios in biological tissues cannot be used to pin-point precise locations on the landscape, but rather, can provide general associations within regions variation as the $^{87}Sr/^{86}Sr$ will represent a homogenization of values from multiple locations.

As mentioned in the beginning of this chapter, Douglas et al. (2013) demonstrated that $^{87}Sr/^{86}Sr$ varies in hydrological systems based on seasonal temperature, precipitation, and permafrost levels, and this could potentially confound studies seeking to reconstruct seasonal mobility in the past. Interestingly, the $^{87}Sr/^{86}Sr$ seasonal values for the modern specimens vary in a roughly sinusoidal pattern. Without the context of the bison migratory behavior, the results would be suggestive that the seasonal $^{87}Sr/^{86}Sr$ variation might be a result of changes in the hydrological cycle. However, the fact that seasonal variation in $^{87}Sr/^{86}Sr$ values for the specimens matches the variation of $^{87}Sr/^{86}Sr$ in the different habitat areas is a strong indication that the sinusoidal pattern is resulting from actual movement across the landscape between regions of higher ratios in the summer and regions of lower ratios in the winter. If a similar pattern appears for the prehistoric samples, it would be difficult to determine whether it is a product of actual movement across the landscape or from freeze/thaw effects in the hydrological cycle. This effect is not measurable however, and provided that the $^{87}Sr/^{86}Sr$ values for the prehistoric samples have variable patterns, it will be assumed that the $^{87}Sr/^{86}Sr$ signatures are a result of actual movement across the landscape.

6.5 Summary

The purpose of this modern control study was to determine if serially-sampling bison teeth and measuring the individual samples for $^{87}Sr/^{86}Sr$ and $\delta^{18}O$ was a reliable way to characterize migratory behavior on a seasonal basis for a herd with known migratory patterns. The modern dataset was composed of three molars from two modern *B. b. bison* which spent their lives in the Delta Region. The bison follow known migratory patterns, spending winters along the Tanana and Delta Clearwater Rivers and spring and summers along the Delta River and associating flood plain. The $\delta^{18}O$ results demonstrated clear a sinusoidal pattern, and indicated that using $\delta^{18}O$ as a seasonal proxy was a reliable method for determining peak warm and cool seasons. Additionally, the $^{87}Sr/^{86}Sr$ results tracked very well with the modeled $^{87}Sr/^{86}Sr$ variation in the seasonal habitat areas (Bataille et al. 2014). This control study strongly suggests that these methods are appropriate for characterizing steppe bison behavioral ecology during the Pleistocene. The results for the prehistoric specimens are discussed in the next chapter.

CHAPTER 7: RESULTS AND DISCUSSION

The results of the $^{87}Sr/^{86}Sr$, $\delta^{18}O$ and $\delta^{13}C$ analyses for the prehistoric samples are discussed in this chapter. Based on the expectations from the strontium and oxygen isoscapes (Bataille et al. 2014 and Sloat 2014, respectively) the results fit the expected range of variation for the isotope values, and there is no indication that the results were contaminated. Sample means and standard deviation (SD) are employed as descriptive statistics. Because the samples are from two separate locations in the YTU - the CRREL permafrost tunnel and Lost Chicken Creek - and therefore these sample datasets will be discussed separately (although all samples are frequently presented together in the same tables and graphs). The Lost Chicken Creek samples are compared temporally as well to determine if there were changes over time in bison behavior. Summary statistics, including the mean, standard deviation (SD), range, and amplitude (Amp.) for each of the samples is presented in Table 5 (see Appendix B for the raw values).

7.1 Assessing Contamination

While tooth enamel is one of the densest and least susceptible skeletal materials to diagenesis (see Section 4.1.3; Budd et al. 2000; Fox and Fisher 2004; Hoppe et al. 2003; Kohn et al. 1999), isotope values can still be altered due to contamination resulting from sampling or analytical error. While this study did not specifically assess preservation, all of the teeth were visibly well preserved and had an appearance that was indistinguishable from modern bison dentition. All skeletal material recovered from both the CRREL permafrost tunnel and Lost Chicken Creek show remarkable preservation for numerous species and bone material (Harington 1980; Porter 1988; US Army Corps of Engineers), providing an indication that

Table 5. Summary Isotope Values for Prehistoric Specimens[6]. The mean, standard deviation (SD), and range for $^{87}Sr/^{86}Sr$ is presented in the following table, and the same summary statistics, along with amplitude (Amp.) is presented for $\delta^{18}O$ and $\delta^{13}C$ for each of the specimens. Standard deviation is determined as the standard deviation of the specimen mean value. Amplitude is determined as the difference between the highest and lowest values for that specimen. # Samp. Removed indicates how many individual serial-samples were removed from that tooth. Teeth are M_3's unless otherwise noted.

Sample ID	# Samp. Removed	$^{87}Sr/^{86}Sr$			$\delta^{18}O$ (‰)[7]				$\delta^{13}C$ (‰)[8]			
		Mean	*SD*	*Range*	*Mean*	*SD*	*Range*	*Amp.*	*Mean*	*SD*	*Range*	*Amp.*
UAMES-6335	8	0.71018	0.00062	0.70908 - 0.71081	-21.4	0.8	-22.4 to -20.3	2.1	-11.3	0.2	-11.7 to -11.1	0.6
CRREL-FPT	6	0.71242	0.00004	0.71236 - 0.71247	-16.7	0.8	-18.2 to -15.9	2.3	-10.3	0.2	-10.6 to -10.0	0.7
UAMES-6173	8	0.71111	0.00005	0.71106 - 0.71123	-20.1	0.5	-20.8 to -19.3	1.5	-11.0	0.2	-11.4 to -10.5	0.9
UAMES-6768	8	0.70917	0.00006	0.70909 - 0.70926	-19.6	0.3	-20.2 to -19.3	0.9	-9.8	0.2	-10.1 to -9.3	0.9
UAMES-6377	11	0.71303	0.00044	0.71259 - 0.71386	-19.8	0.7	-20.7 to -18.3	2.4	-10.1	0.1	-10.3 to -10.1	0.2
UAMES-6602	8	0.70823	0.00009	0.70813 - 0.70842	-22.2	0.4	-22.7 to -21.5	1.2	-10.2	0.2	-10.5 to -9.9	0.6
UAMES-6620	9	0.70821	0.00019	0.70799 - 0.70864	-20.3	0.7	-21.7 to -19.4	2.2	-10.3	0.4	-10.7 to -9.6	1.1
UAMES-6616	8	0.71186	0.00061	0.71097 - 0.71265	-21.3	0.5	-22.2 to -20.7	1.4	-10.5	0.2	-10.7 to -10.2	0.6
UAMES-6785	7	0.70787	0.00002	0.70783 - 0.70790	-19.8	0.5	-20.6 to -19.0	1.6	-11.1	0.2	-11.4 to -10.7	0.7
UAMES-12224	6	0.70691	0.00016	0.70671 - 0.70720	-20.9	0.7	-21.9 to -20.0	1.9	-11.0	0.2	-11.3 to -10.8	0.5
UAMES-6382	6	0.70784	0.00008	0.70774 - 0.70796	-20.6	0.4	-21.1 to -20.1	1.0	-11.4	0.1	-11.7 to -11.2	0.4
UAMES-8582	6	0.71036	0.00007	0.71025 - 0.71043	-21.3	0.5	-22.0 to -20.7	1.3	-11.0	0.1	-11.1 to -10.9	0.2
UAMES-6594	8	0.70966	0.00007	0.70959 - 0.70982	-21.5	0.7	-22.6 to -20.4	2.2	-11.8	0.2	-12.0 to -11.4	0.7
UAMES-6599	7	0.70886	0.00004	0.70878 - 0.70891	-20.5	0.5	-21.6 to -20.0	1.5	-11.1	0.2	-11.2 to -10.9	0.4

* Represents M_2's

**Mean, SD, Range, and Amplitude of this specimen does not include the 4th sample which had very high values indicating the sample may have been contaminated

[6] Unless otherwise noted, all graphs and tables are aligned chronologically in this chapter. For tables, the youngest specimen (UAMES-6335) is at the top and the specimens get chronologically older moving down the page, ending with the oldest specimen (UAMES-6599). For graphs, the youngest specimen is graphed on the left, and the specimens get chronologically older moving across the page from left to right, ending with the oldest specimen.

[7] All oxygen stable isotope ratios in this chapter are normalized with respect to Vienna Standard Mean Ocean Water (V-SMOW).

[8] All carbon stable isotope ratios in this chapter are normalized with respect to Vienna Pee Dee Belemnite (VPDB).

dental enamel likely was well preserved in those deposits. None of the samples - with the exception of CRREL-FPT which was stained a dark grey-blue - showed any visible discoloration besides slight yellowing. However, there were several small micro-fissures in the teeth, which could not be avoided during sampling and some of the drilled matrix was removed from near these fissures.

While not a traditional measure of contamination, the $\delta^{13}C$ values for the three M_2's show nearly identical patterns when graphed (see Figure 18). The M_2's would have formed during the nursing and weaning period, and therefore should demonstrate a distinctive pattern in $\delta^{13}C$ values as there is a small trophic increase from mother to offspring (on the scale of ~1‰; e.g., Balasse 2002; Gadbury et al. 2000). This is a strong indication that the isotope values are reflective of the true values which would have been mineralized at similar times during the growth and development for each bison. It is unlikely that the three teeth would have undergone contamination processes that would have affected them in an identical way. Based on this, it is assumed that contamination of the $\delta^{13}C$ values is minimal for all of the LCC specimens. Additionally, because the $\delta^{18}O$ values were analyzed simultaneously with the $\delta^{13}C$ values, and the $\delta^{18}O$ values match the expected range (e.g., Sloat 2014), the $\delta^{18}O$ results are assumed to be reflective of the true values as well. One exception to this was the fourth sample removed from specimen UAMES-6599 (sample # 6599-4) which had much lower $\delta^{13}C$ and $\delta^{18}O$ than the rest of the samples for that individual (see Figure 19). It was assumed that this was due to sample contamination or analytical error, and this sample is not included in the discussion of results or presented in any further graphs. The $\delta^{13}C$ and $\delta^{18}O$ values for the CRREL specimen generally match the expectations for the range of variation (Sloat 2014; Wooller et al. 2007), and therefore,

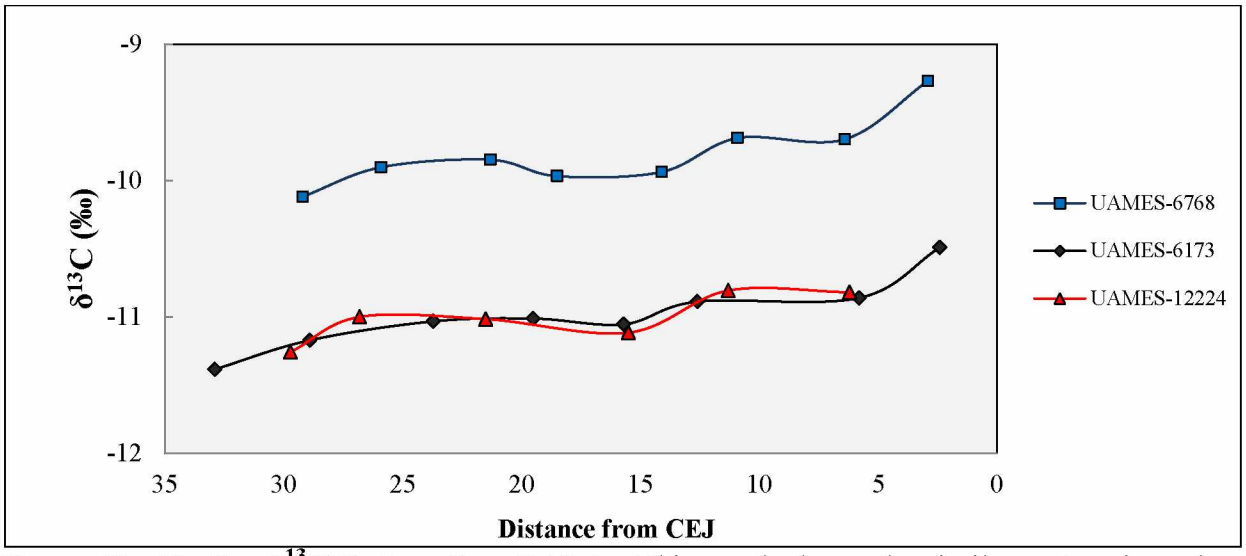

Figure 18. Similar $\delta^{13}C$ Pattern for all M_2's. This graph shows the similar pattern in carbon isotope values for the three prehistoric M_2's. The patterning is assumed to represent formational processes related to the nursing/weaning signal.

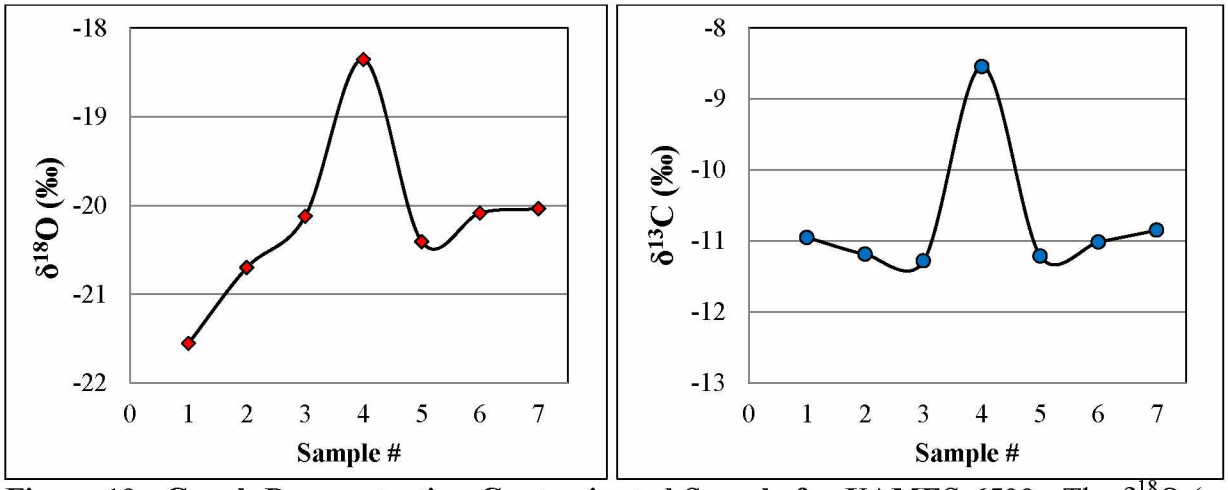

Figure 19. Graph Demonstrating Contaminated Sample for UAMES-6599. The $\delta^{18}O$ (red) and $\delta^{13}C$ (blue) values for sample #4 displays significantly higher values than the rest of the samples that were removed from this tooth.

is also assumed to not be contaminated. Previous research (e.g., Bocherens et al. 1994; Fox and Fisher 2004; Kohn et al. 1999) has demonstrated that $^{87}Sr/^{86}Sr$ values can be considered reliable in tooth enamel, and Hoppe et al. (2003) demonstrated that ~95% of diagenic strontium is removed with pretreatment methods, suggesting that $^{87}Sr/^{86}Sr$ values measured in tooth enamel should be reliable. Additionally, the results match the expected variation for the regions of study; therefore, the $^{87}Sr/^{86}Sr$ values are assumed to be reliable.

7.2 Incremental Analysis

One factor that can be problematic with serial-sampling techniques is lining up the individual samples from multiple specimens so the results can be meaningfully compared. In this study, care was taken to ensure that samples were removed from the same location on each tooth. However, the samples were removed with relatively large tools (Dremel and 1 mm diamond-coated Dremel bit) which were used free-hand and did not have a guide, with the exception of a line indicating the location of where each sample should be placed on the transverse portion of each tooth. Although the samples were carefully drilled out, there will be some inter-sample error in the placement.

Some published studies have assumed that the margin of error caused by this sampling strategy is small enough that there is no need to correlate further, and that the samples from separate teeth can simply be aligned by sample number (1^{st} sample, 2^{nd} sample, and so on; i.e., Britton et al. 2009, Britton et al. 2011; Fricke and O'Neil 1996; Gadbury et al. 2000; Stevens et al. 2011). Others have lined the samples up relative to the distance from the cemento-enamel junction (CEJ) on each tooth (e.g., Bernard et al. 2009; Feranec et al. 2009; Fisher and Valentine

2013; Fricke et al. 1998; Gadbury et al. 2000; Higgins and MacFadden 2004; Julien et al. 2012; Pellegrini et al. 2008). This method assumes that birth synchronicity is constant and that inter-individual developmental differences are minimal. Under these assumptions, the CEJ will represent the same location, physically and developmentally, on each tooth. Widga (2006) developed a third method for lining up serial samples by tooth row length, which takes into account herd variability and inter-individual formational differences. Widga (2006) and Widga et al. (2010) have criticized aligning samples based on sample location or distance from CEJ because of differential mineralization processes; however, their method was designed for use with a large number of samples, often using multiple teeth from a single bison, and from temporally constrained sites. Additionally, their method also was specifically designed for mid-latitude herds that demonstrate more variable calving patterns.

Because this study encompasses only one tooth from each individual, covers a relatively long timespan (~35,000 years), cannot be considered a population *sensu* Widga (2006), and because the samples are from a high-latitude environment, 'distance from CEJ' is the method used for lining up the inter-individual samples (distance from CEJ for each sample is presented in Appendix B). Changes in temperature and precipitation regimes over the course of the ~35,000 years represented by this dataset may have altered calving patterns by weeks or even months, and there are likely formational differences in individual mineralization processes which off-set the isotopic signals. However, because the specimens are evaluated individually, rather than treating them as representing a herd (except when addressing change over time in Section 7.7.3, which again, does not suggest that the dataset comprises a herd), inter-individual differences are considered insignificant in this study.

7.3 Strontium Results

The strontium results for all individuals show variation in the fourth or fifth decimal. The mean, SD, and range for each specimen are presented in Table 5 (see Appendix B for the raw sample values for each specimen). Studies that have addressed migration consider variation of $^{87}Sr/^{86}Sr$ values to be significant at the fifth decimal (*c.f.,* Bentley 2006; Price et al. 2002). There is a significant amount of variation within a small radius (~15 km) around both prehistoric sample locations - the CRREL Permafrost Tunnel and the Lost Chicken Creek locality - which are displayed in Figure 9 and Figure 10. The predicted range for $^{87}Sr/^{86}Sr$ in a 50 km radius around the CRREL Permafrost Tunnel is between 0.70580 and 0.76462 (Bataille et al. 2014). Specimen CRREL-FPT has a mean ratio of 0.71242 ±0.0006 which matches this expectation, and suggests that this bison lived within 50 km of where it was found.

The $^{87}Sr/^{86}Sr$ values for the LCC samples range between 0.70678 and 0.71386 for a total variation of 0.00708. The total predicted variation in $^{87}Sr/^{86}Sr$ values within a 50 km radius around the Lost Chicken Creek locality (LCC) is between 0.70388 and 0.71114 (Bataille et al. 2014), and while some of the specimens have $^{87}Sr/^{86}Sr$ ranges that match this, several of them have higher ratios. A 50 km radius from the sample locales was arbitrarily chosen, but is was based on the maximum range of mobility that the Delta herd displays on a seasonal basis (see Chapter 6). Expanding the radius around LCC to 100 km provides a larger range of predicted $^{87}Sr/^{86}Sr$ values, between 0.70383 and 0.74487 (Figure 20). This larger radius encompasses all of variation for the LCC specimens, and indicates that the region southwest of the locale has values in the same range as all of the specimens. Specifically, the river basins associated with the Fortymile River, including the Mosquito Fork River and tributaries, Molly Creek and tributaries, and the West Fork of the Dennison Fork River and tributaries encompass the range of

variation that is seen in the LCC dataset (Figure 21). There is no other region that as effectively encompasses the range of variation. While only subjective, this suggests that these river basins could have provided bison habitat area.

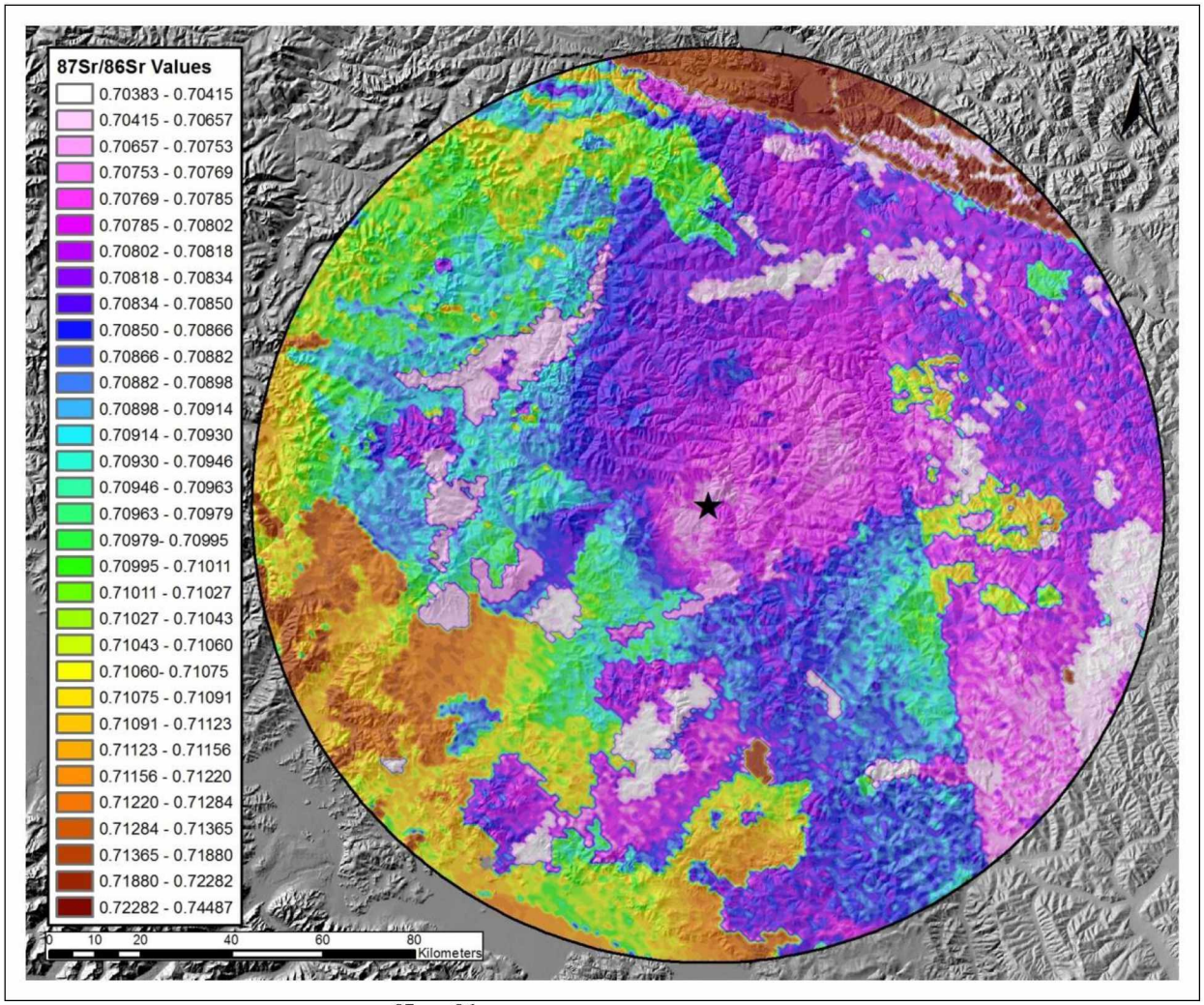

Figure 20. Isoscape Showing $^{87}Sr/^{86}Sr$ Variability within a 100 km radius around the Lost Chicken Creek Locality. Black star marks Lost Chicken Creek. Derived from the Bataille et al. (2014) raster dataset.

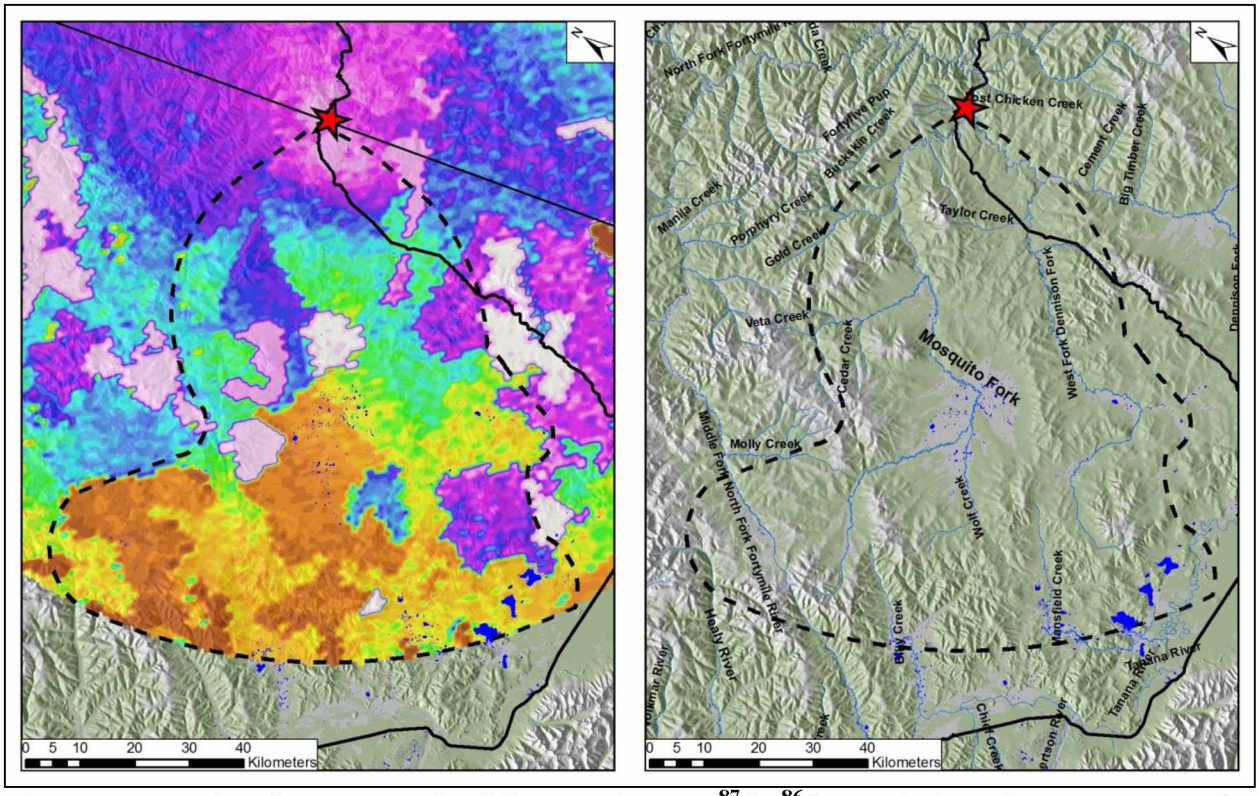

Figure 21. Region Southwest of LCC Matching the $^{87}Sr/^{86}Sr$ Variation of the Dataset. The map on the right displays the variation in $^{87}Sr/^{86}Sr$ values (the colors match the values as in Figure 20) and the map on the right displays the topography and hydrography of the region.

7.3.1 Identifying Non-Local Individuals at Lost Chicken Creek

A standard method for determining local vs. non-local individuals based on $^{87}Sr/^{86}Sr$ values is to use two standard deviations (SD) of the population mean to identify the 'local' signature; any samples or individuals that fall outside of this range are considered non-local (*c.f.*, Price et al. 2002). However, this method has typically been applied to studies that have much tighter chronological control than this study (i.e., hundreds of years to a few thousand years), and typically use samples from more controlled depositional environments such as archaeological excavations (e.g., Bentley 2004; Bentley and Knipper 2005; Ezzo et al. 1997; Haverkort et al. 2008). Because the LCC specimens encompass a high degree of variation, two SD of the population would encompass all of the specimens in the dataset (two SD = 0.00180).

Additionally, the prehistoric samples derive from alluvial deposition and many specimens are separated by several thousand years, making this dataset less controlled than many studies that use SD as the criteria for determining local $^{87}Sr/^{86}Sr$ signatures. Therefore, non-local individuals have been identified in this study as falling outside of one SD of the normalized mean for the dataset (for the LCC specimens; the CRREL-FPT specimen was not included in this dataset). This is a more rigorous and critical method for determining non-local signatures as it decreases the range. The results are presented in Figure 22, and indicate that specimens UAMES-6377, UAMES-6616, and UAMES-12224 are non-local individuals. Furthermore, samples within specimens UAMES-6785 and UAMES-6382 fall outside of one SD, but not the entire specimen.

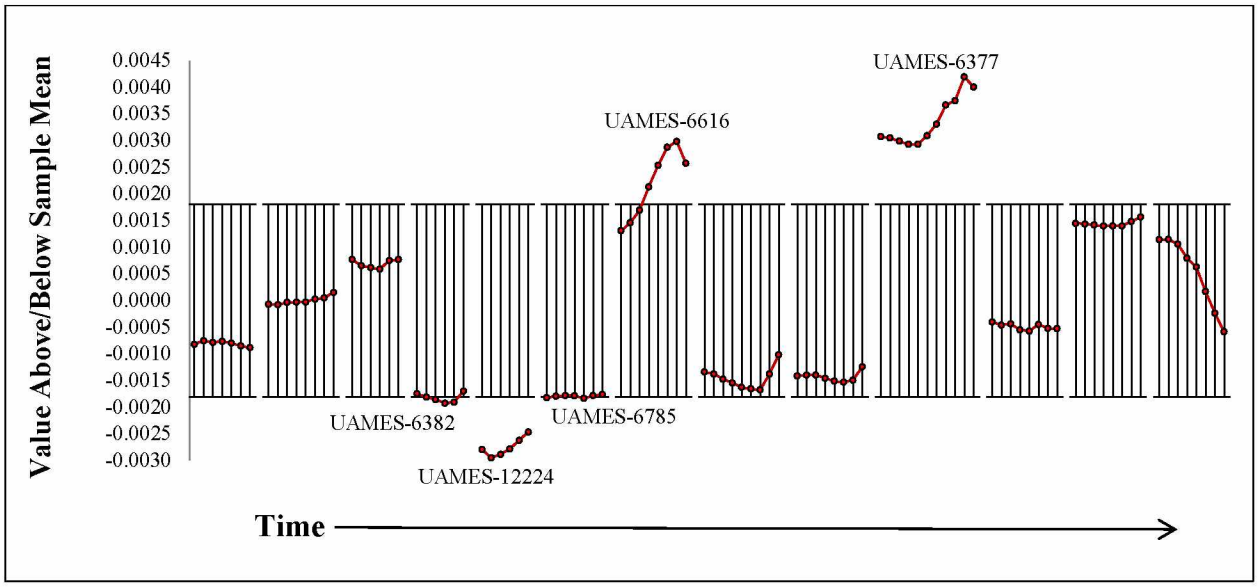

Figure 22. Graph Showing Non-local vs. Local LCC Specimens. This graph shows the normalized sample value above or below the population mean for LCC. The black bars indicate one standard deviation of the sample mean for the LCC dataset.

7.3.1.1 Mean $^{87}Sr/^{86}Sr$ Gradient around Lost Chicken Creek

The tooth $^{87}Sr/^{86}Sr$ values are also presented relative to a profile of the mean $^{87}Sr/^{86}Sr$ values radiating from the Lost Chicken Creek locality at 10 km arcs (see Figure 23). The profile was created by methods developed in this study which included buffering sequential rings up to 110 km away, spaced at 10 km apart, around the LCC locality in ArcGIS 10.2, and then those rings were used to clip the $^{87}Sr/^{86}Sr$ raster dataset produced by Bataille et al. (2014). The resulting raster rings were then divided into halves (trending generally north-south) to produce 10 km wide, 180° arcs that show the $^{87}Sr/^{86}Sr$ variation around Lost Chicken Creek. The dividing line for the two halves was not arbitrarily chosen: in general, the $^{87}Sr/^{86}Sr$ values to the northeast of LCC are relatively low with a small SD, while the $^{87}Sr/^{86}Sr$ values to the southwest of LCC are relatively high with greater variation. This dividing line was chosen to separate regions of relatively higher and lower ratios, so as to prevent dampening the mean value for each 10 km arc and to reduce the SD as much as possible. The mean $^{87}Sr/^{86}Sr$ values for each arc ($\overline{X}$ Sr_{arc}) were then calculated and plotted in Figure 23. Finally, the mean ratios for each of the LCC samples were then plotted on the same graph, and the x-axis value for each specimen was adjusted so that the specimen mean would bisect the $\overline{X}$ Sr_{arc} mean trendline (the x-axis displays kilometers southwest or northeast of LCC).

This method provides a way to determine general sub-regional associations for the specimens, and the samples have means that trend to the southwest of LCC. None of the specimens have mean values that are located solely to the northeast; specimens UAMES-6602, UAMES-6620, UAMES-6785, and UAMES-6382 have means that are found both to the southwest and to the northeast of the LCC locality, but have means that are can be found within a

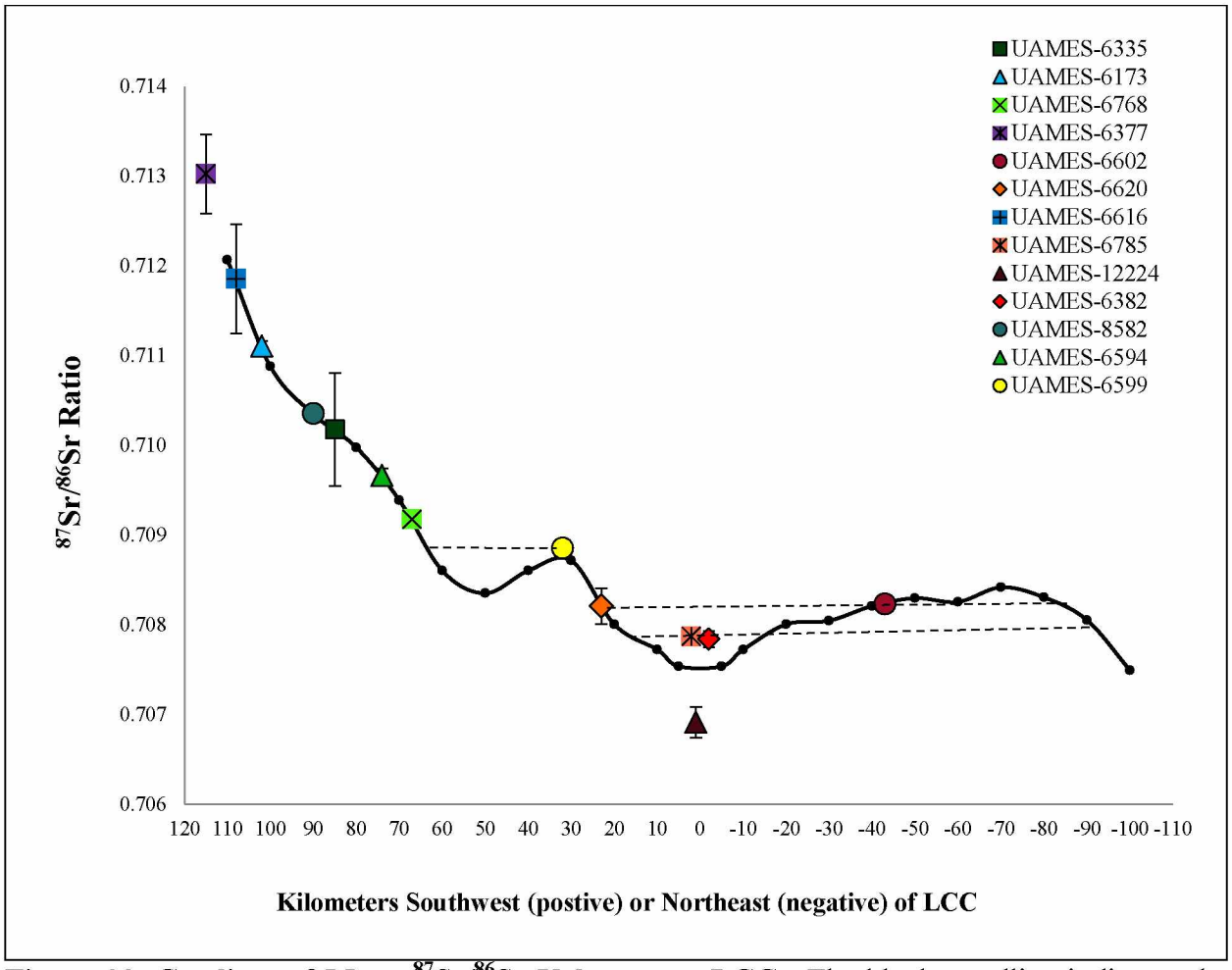

Figure 23. Gradient of Mean $^{87}Sr/^{86}Sr$ Values near LCC. The black trendline indicates the mean $^{87}Sr/^{86}Sr$ values in 10 km wide, 180° arcs around Lost Chicken Creek ($\overline{X}$ Sr_{arc}). Zero on the x-axis indicates the locality. Where possible, the specimen means are centered over the $\overline{X}$ Sr_{arc} trendline. Error bars for the specimens indicate the standard deviation for that sample mean. The three dashed lines indicate multiple geographical regions that UAMES-6620 and UAMES-6602, and UAMES-6785 and UAMES-6382 could be associated with, respectively.

30 km radius in either direction. Specimens UAMES-6377 and UAMES-12224 have sample means outside of the $\overline{X}$ Sr_{arc} values. Interestingly, both of these specimens fell outside of one SD of the normalized sample mean for LCC, and this matches the expectations for those specimens representing non-local individuals. While it would be easy to infer that both of these specimens must have lived outside of the 110 km radius around LCC, the SD for the $\overline{X}$ Sr_{arc} is

measured on the second and third decimal, indicating a high degree of regional variability (see Appendix C for list of SD for each $\overline{X}$ Sr_{arc}). Additionally, the area encompassed by each 10 km arc increases exponentially, and by the time the $\overline{X}$ Sr_{arc} value is calculated for the 110 km arc, it is derived from a wide range of $^{87}Sr/^{86}Sr$ ratios. Even though UAMES-6377 and UAMES-12224 have means outside of the trendline, the $^{87}Sr/^{86}Sr$ ratios for those samples can still found within a 100 km radius of LCC, but are restricted to very localized regions (i.e., ~5 to 30 km^2). Regions with low $^{87}Sr/^{86}Sr$ values similar to UAMES-12224 are located predominantly to the southeast and east of LCC, while regions with the high $^{87}Sr/^{86}Sr$ values similar to UAMES-6377 are located predominantly to the southwest and west of LCC.

7.3.1.2 Mean $^{87}Sr/^{86}Sr$ Gradient around the CRREL Permafrost Tunnel

A gradient of the mean $^{87}Sr/^{86}Sr$ values in 10 km increments around the CRREL permafrost tunnel was also created using the same methods as Section 7.3.1.2, up to 50 km away from the locale. A dividing line separating the rings into 180° arcs was also chosen to split the region into two portions of relatively similar $^{87}Sr/^{86}Sr$ distribution. The dividing line runs at approximately 45°, dividing the region into a northwest portion and a southeast portion, and was chosen in an attempt to prevent damping of the mean $^{87}Sr/^{86}Sr$ ratios and to decrease the SD as much as possible. Specimen CRREL-FPT was then added to the graph (

Figure **24**); however, the specimen has a lower $^{87}Sr/^{86}Sr$ mean than any of the $\overline{X}$ Sr_{arc} values. Ratios that match CRREL-FPT are found in very localized areas (~4 to 12 km^2) approximately 15 km west-southwest of the locality in relatively low elevation mountains and valleys along Goldstream Creek and the Chatanika River valley (see Figure 9). Similar values are also found ~40 km to the north of the CRREL Tunnel, in less localized regions at the headwaters of the

Tolovana River and Victoria Creek, but the region between there and the CRREL Tunnel have significantly different $^{87}Sr/^{86}Sr$ ratios from the specimen.

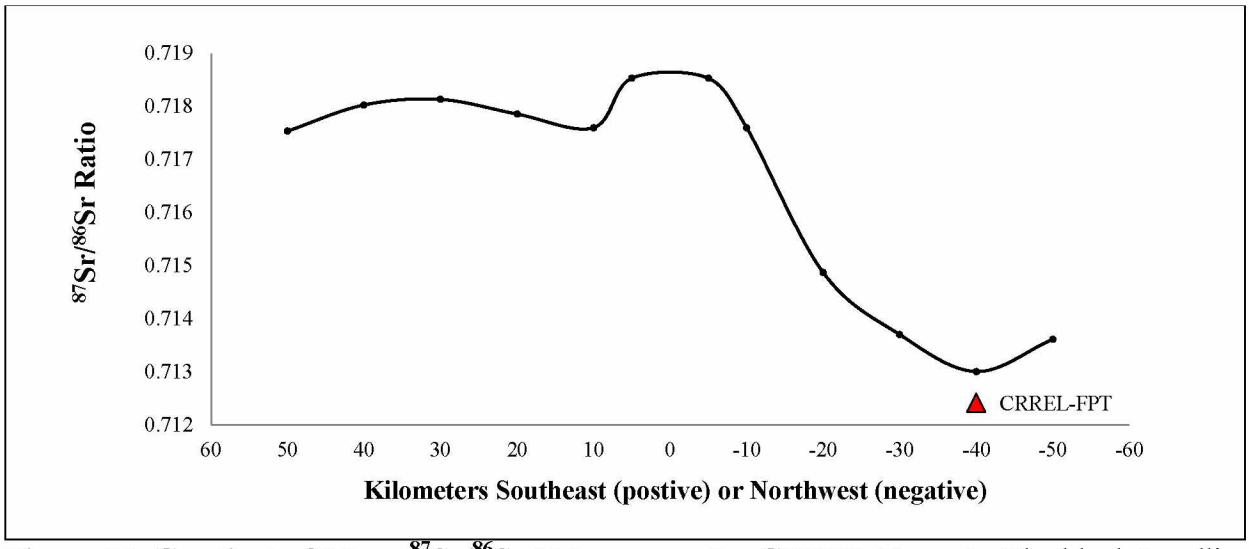

Figure 24. Gradient of Mean $^{87}Sr/^{86}Sr$ Values near the CRREL Tunnel. The black trendline indicates the mean $^{87}Sr/^{86}Sr$ value in 10 km wide 180° arcs around the CRREL Tunnel ($\overline{X}$ Sr_{arc}). Zero on the x-axis indicates the locality. Error bars for specimen CRREL-FPT have been graphed, but are not large enough to be visible.

7.3.2 Defining Migratory Signatures

There is no standard method for identifying seasonal migration. Changes in geographical location over time is typically determined by matching the sample $^{87}Sr/^{86}Sr$ values with local or regional variation near the sample locale, or by using two standard deviations of the population mean to identify non-local individuals (e.g., Britton et al. 2011; Haverkort et al. 2008; Julien et al. 2012), but there is no commonly-used statistical method for quantifying migratory signatures. Additionally, many paleo-studies that have used $^{87}Sr/^{86}Sr$ to reconstruct migration have used coarse-scale strontium isoscapes, and can only provide gross associations of $^{87}Sr/^{86}Sr$ increases

or decreases over large geographical regions (i.e., Fisher and Valentine 2013; Pellegrini et al. 2008; Thornton 2011; Widga 2006). For many studies, regional associations of $^{87}Sr/^{86}Sr$ increases or decreases are sufficient for the research questions at hand; however, for identifying seasonal changes and small-scale landscape use-patterns this method is insufficient. Therefore, a different method for defining migration was developed for this study.

While significance is measured in the fifth decimal for $^{87}Sr/^{86}Sr$ (*c.f.*, Bentley 2006), variation in ratios up to the third decimal can occur in very small regions (~5-15 km^2) around both the CRREL permafrost tunnel and the Lost Chicken Creek locality (Bataille et al. 2014). Because of this localized variation, the samples were not evaluated together as a population because individual specimens theoretically could have widely variable $^{87}Sr/^{86}Sr$ values, even if relatively similar locations on the landscape had been utilized. Because of the variability of the landscape, the variability in the specimen $^{87}Sr/^{86}Sr$ ranges and ages, and given access to a high-resolution strontium isoscape (Bataille et al. 2014), each specimen was treated separately. Each of the specimens was considered a single dataset, and the individual serial-samples from that specimen were considered a sub-population. One method to help visualize the data involved normalizing the data from each tooth relative to the specimen mean, and any values falling outside of one SD of the normalized specimen mean was considered to be a 'migratory' $^{87}Sr/^{86}Sr$ signature. As emphasized in Chapter 1, the term "migratory" does not inherently mean a large-scale change, but is used in this study to simply indicate a change in physical location.

This method allows each specimen to be evaluated independently of one another but at the same scale, and indicates any values that vary significantly from the rest of the values within that sub-dataset (tooth). The results of this approach are displayed in Figure 25, and show that all of the specimens include values that fall outside of one SD of the specimen mean; these

values are usually associated with the oldest or the youngest serial-sample (although, some specimens have samples from the middle of the sequence that fall outside of one SD). When graphed, the results also demonstrate that some of the specimens have standard deviations well above the mean (UAMES-6335 for example), while some have small standard deviations lying just outside of one SD (CRREL-FPT for example). This is only qualitatively addressed in this study, but specimens with values 'well' outside one SD (i.e., on the scale >0.001: UAMES-6335, UAMES-6377, UAMES-6620, and UAMES-6616) are assumed to represent individuals that moved greater distances than specimens with values falling on the line or "just" outside (i.e., <0.001) of one SD. Based on generalized enamel mineralization patterns, the values falling outside of one SD at the beginning or the end of the sequence incorporate isotope values from a

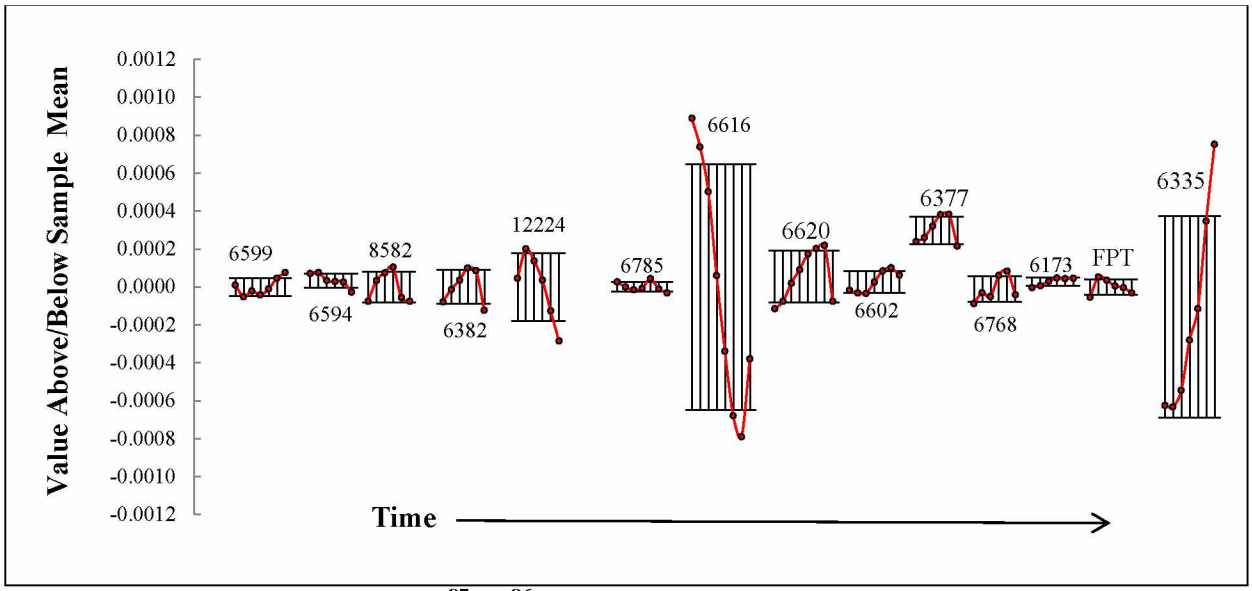

Figure 25. Seasonal Migratory $^{87}Sr/^{86}Sr$ Signatures for the Prehistoric Specimens. Error bars represent one standard deviation (SD) of the sample mean. Migratory samples are defined as falling outside of one SD of the normalized sample mean. Specimen labels have been abbreviated to the numerical portion for the LCC samples, while the CRREL sample has been abbreviated to FPT.

different season than the rest of the samples, providing an indication that there was some degree of seasonal migration. Figure 25 illustrates this, and demonstrates that some specimens show very little change while others show a large amplitude of change throughout the developmental period of the tooth. However, no effort is made to quantify this migration, other than to say migratory behavior likely occurred, albeit on a small scale (<700 km^2). The association between this migratory behavior and seasonality is further discussed in Section 7.5.1, and is contextualized with regards to human landuse patterns in Chapter 8.

7.4 Environment and Seasonality: The $\delta^{18}O$ and $\delta^{13}C$ Results

Based on the $^{87}Sr/^{86}Sr$ results, it seems that some teeth illustrated small-scale changes in geographical location for steppe bison on a seasonal basis. The $\delta^{18}O$ and $\delta^{13}C$ results provide additional behavioral and environmental context for the specimens. Because oxygen isotopes are tied to the meteoric water cycle, $\delta^{18}O$ values vary based on precipitation and temperature changes, and can be used to identify small-scale seasonal changes as well as climate changes on a global level (e.g., Gat 1996). The ratio of carbon isotopes in biological organisms is a reflection of diet (e.g., Lee-Thorpe 2008; Koch 2007), but can be used as a proxy for reconstructing climate and vegetation regimes as well (e.g., Marshall et al. 2007). The mean, SD, range, and amplitude for $\delta^{18}O$ and $\delta^{13}C$ for each specimen is presented in Table 5 (see Appendix B for the raw values).

Based on the isoscape published by Sloat (2014), the estimated range of variation for the YTU and Tanana Basin is between -19.0‰ and -24.0‰, with lower values in mountainous areas, and higher values in valleys and basins (see Figure 7). The range of $\delta^{18}O$ values for the prehistoric samples were similar to the expected range (varying between 5-6‰). The amplitude

within the teeth ranged from a maximum of 2.4‰ to a minimum of 0.9‰. However, based on published values from mid-latitude regions, the predicted amplitude for the $\delta^{18}O$ seasonal signature in Pleistocene-aged bison teeth is expected to be approximately 4-5‰ (Bernard et al. 2009; Higgins and MacFadden 2004; Julien et al. 2012). A higher amplitude is predicted as the seasonal sinusoidal variation increase with increasing latitude (e.g., Fricke et al. 1998). However, in studies of modern ungulates in Alaska, the actual amplitude of the $\delta^{18}O$ seasonal signature is slightly less than predicted. Based on the amplitude from modern caribou on the North Slope (Britton et al. 2009) and modern bison from this study (Chapter 6), the mean $\delta^{18}O$ amplitude for Alaskan ungulates is ~3‰.

The CRREL-FPT specimen had $\delta^{18}O$ values ranging between -15.9‰ and -18.2‰ with a mean of -16.7‰ (see Table 5). The amplitude for the CRREL-FPT specimen was 2.3‰, which is slightly lower than the $\delta^{18}O$ amplitudes in Pleistocene-aged bison teeth from mid-latitude regions, or from modern specimens in Alaska. The $\delta^{18}O$ results for the LCC specimens range between -18.3‰ and -22.6‰ (see Table 5), while the amplitudes ranged between 0.9‰ and 2.2‰, again demonstrating less variation than mid-latitude environments, and less than ungulates for high-latitude environments. This suggests that there was an environmental mechanism or behavioral trait that created greater homogenization of $\delta^{18}O$ values between summer and winter season.

One possible explanation for the low amplitude is relatively homogenous temperatures throughout the Pleistocene which would have contributed to the more homogenous $\delta^{18}O$ patterns. However, $\delta^{18}O$ values in teeth also reflect precipitation $\delta^{18}O$ values. Changes in $\delta^{18}O$ values between summer rain and winter snow fall should lead to the similar amplitude that is observed in modern ungulates. Alternatively, bison behavior may have been contributing to the dampened

values. Higher elevation areas have relatively lower $\delta^{18}O$ mean annual values while lower elevation areas have relatively higher $\delta^{18}O$ mean annual values (e.g., Bowen et al. 2005). Therefore, if bison were migrating to higher elevation areas during the summer and lower elevation areas during the winter, this would dampen the $\delta^{18}O$ seasonal amplitude as they would be tracking a change in $\delta^{18}O$ values of precipitation over multiple seasons. This matches the seasonal migratory behavior patterns for modern bison in the Tanana Valley (Chapter 6) as well as modern herds in high-latitude and mountainous regions in Canada and Yellowstone Park (Geremia et al. 2011; Grogan et al. 2010; Larter and Gates 1991; Meagher 1973).

Research on Pleistocene-aged sedge and graminoid vegetation from interior Alaska and the Yukon suggests that $\delta^{13}C$ values for the vegetation should range between -27.1‰ and -25.5‰, depending on mesic/xeric conditions and plant habitats (Wooller et al. 2007). The $\delta^{13}C$ values for the CRREL-FPT specimen ranged between -10.6‰ and -9.9‰ with a mean of -10.3‰ (Table 5). The range of values for the LCC specimens was between -12.0‰ and -9.3‰ (Table 5). However, carbon isotopes in teeth have a tissue fractionation factor of around 14.0‰ between product and consumer in carbonate-derived $\delta^{13}C$ values (Cerling and Harris 1999; Balasse 2002; Passey et al. 2005).

Additionally, a slight trophic increase in $\delta^{13}C$ values during the nursing period has been identified in enamel carbonate (Gadbury et al. 2000), indicating that the M_2's used in this study have slightly elevated $\delta^{13}C$ values compared to the M_3's. While this trophic fractionation has not been quantified for bison, Gadbury et al. (2000) refers to this weaning fractionation as being "lower" (less) than 2‰ (Gadbury et al. 2000:86). Therefore, a correction factor of 15‰ has been used in this study for the M_2 specimens. Applying these correction factors to the $\delta^{13}C$ values for all of the prehistoric specimens shows close association to the range of $\delta^{13}C$ values of

graminoids from Aalska as presented by Wooller et al. (2007), and indicates that the steppe bison specimens in this study were grazing on range of plants that varied between -26.0‰ to -24.1‰. This matches expectations from Guthrie (1990) that bison would have grazed on graminaceous vegetation.

7.4.1 Identifying Summer and Winter Seasons

One of the primary reasons that oxygen stable isotopes were analyzed in this study was to have a way to identify peak warm seasons and peak cool seasons within the series of samples for each tooth specimen. In this study, peak summer and peak winter seasons were identified as the highest and the lowest $\delta^{18}O$ values for each of the specimens. Because the same powdered enamel matrix for the $\delta^{18}O$ analysis in each sample was used for the $^{87}Sr/^{86}Sr$ and $\delta^{13}C$ analyses as well, the results of those isotopic ratios can also be correlated to seasons, and thus can provide an indication of seasonal movement and dietary habits. The following figures (Figure 26 through Figure 39) show the correlation between the highest and lowest $\delta^{18}O$ values with the associating $^{87}Sr/^{86}Sr$ and $\delta^{13}C$ values, for all of the prehistoric specimens. The graph at the top of each column represents $\delta^{18}O$ values, and peak high and low values have been correlated with the $^{87}Sr/^{86}Sr$ and $\delta^{13}C$ values which are represented by the middle and bottom graphs in each column, respectively. In general, the trend indicates higher $^{87}Sr/^{86}Sr$ values in winter, and lower $^{87}Sr/^{86}Sr$ values in summer, although not all specimens follow this pattern. However, the data indicate that there were changes in geographical location on a seasonal basis. Additionally, the $\delta^{13}C$ values generally co-vary with $\delta^{18}O$ values, but indicate lower $\delta^{13}C$ values in summer and higher values in winter.

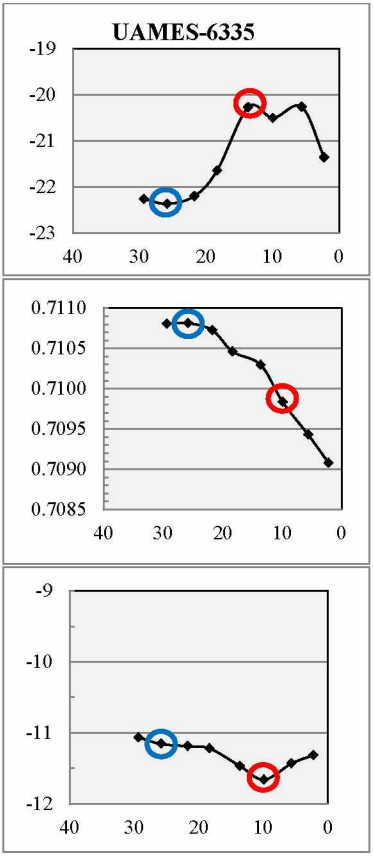

Figure 26. Individual $\delta^{18}O$, $^{87}Sr/^{86}Sr$ and $\delta^{13}C$ Graphs for UAMES-6335. Red circle indicates peak warm season; blue circle indicates peak cool season.

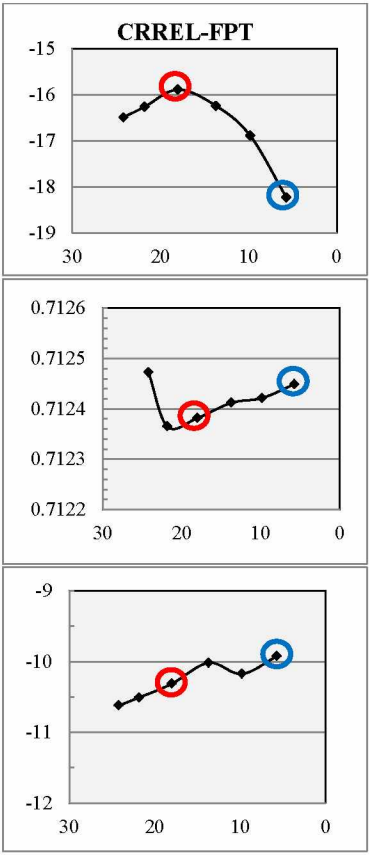

Figure 27. Individual $\delta^{18}O$, $^{87}Sr/^{86}Sr$ and $\delta^{13}C$ Graphs for CRREL-FPT. Red circle indicates peak warm season; blue circle indicates peak cool season.

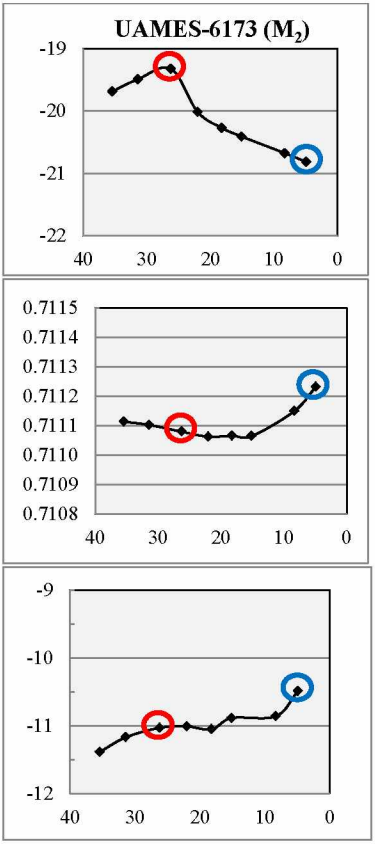

Figure 28. Individual $\delta^{18}O$, $^{87}Sr/^{86}Sr$ and $\delta^{13}C$ Graphs for UAMES-6173. Red circle indicates peak warm season; blue circle indicates peak cool season.

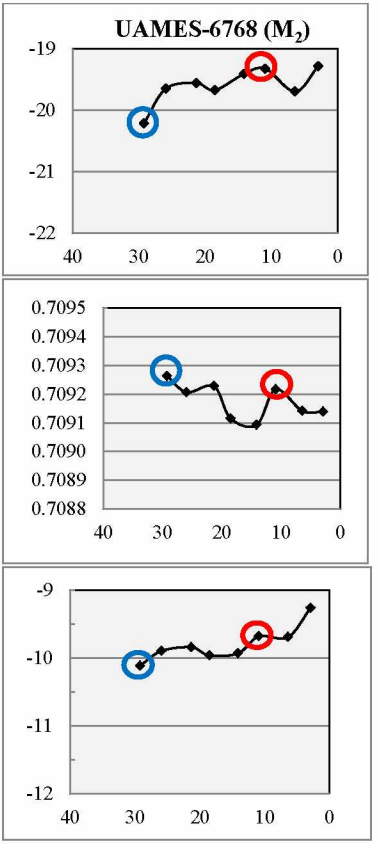

Figure 29. Individual $\delta^{18}O$, $^{87}Sr/^{86}Sr$ and $\delta^{13}C$ Graphs for UAMES-6768. Red circle indicates peak warm season; blue circle indicates peak cool season.

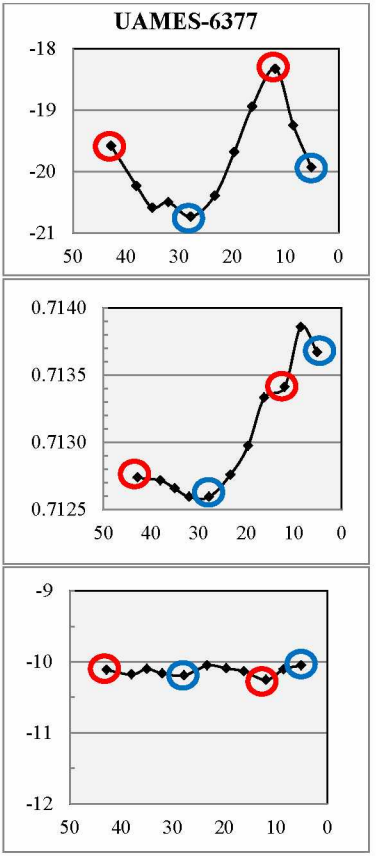

Figure 30. Individual $\delta^{18}O$, $^{87}Sr/^{86}Sr$ and $\delta^{13}C$ Graphs for UAMES-6377. Red circle indicates peak warm season; blue circle indicates peak cool season.

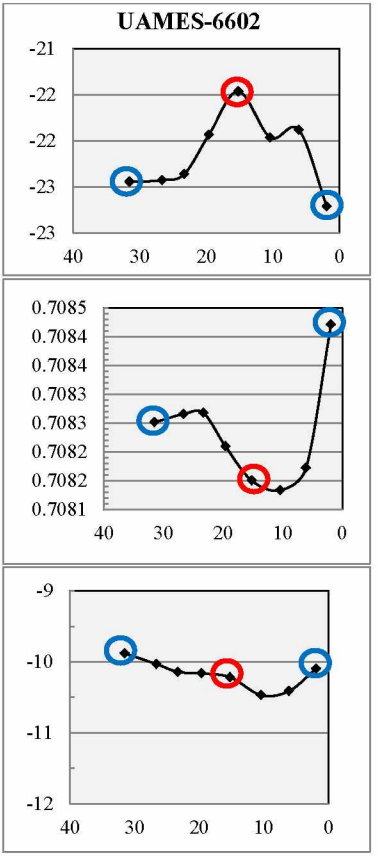

Figure 31. Individual $\delta^{18}O$, $^{87}Sr/^{86}Sr$ and $\delta^{13}C$ Graphs for UAMES-6602. Red circle indicates peak warm season; blue circle indicates peak cool season.

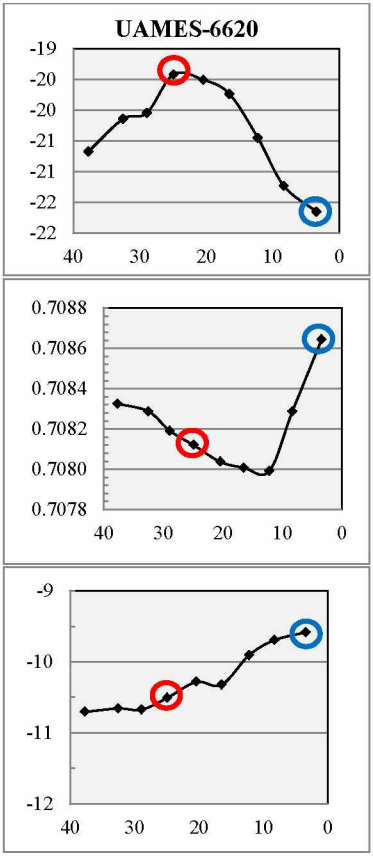

Figure 32. Individual $\delta^{18}O$, $^{87}Sr/^{86}Sr$ and $\delta^{13}C$ Graphs for UAMES-6620. Red circle indicates peak warm season; blue circle indicates peak cool season.

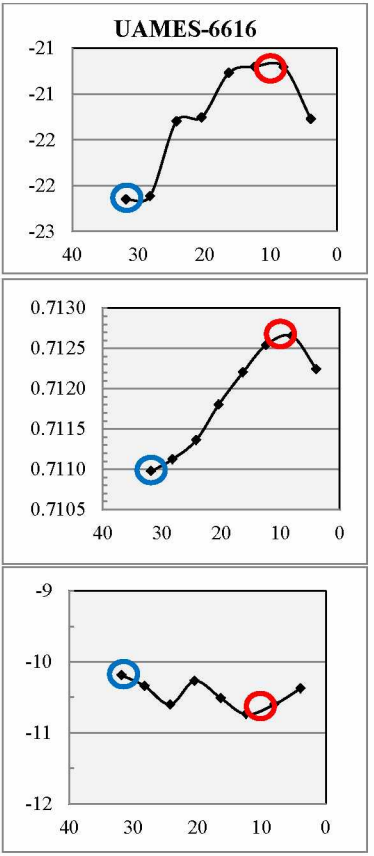

Figure 33. Individual $\delta^{18}O$, $^{87}Sr/^{86}Sr$ and $\delta^{13}C$ Graphs for UAMES-6616. Red circle indicates peak warm season; blue circle indicates peak cool season.

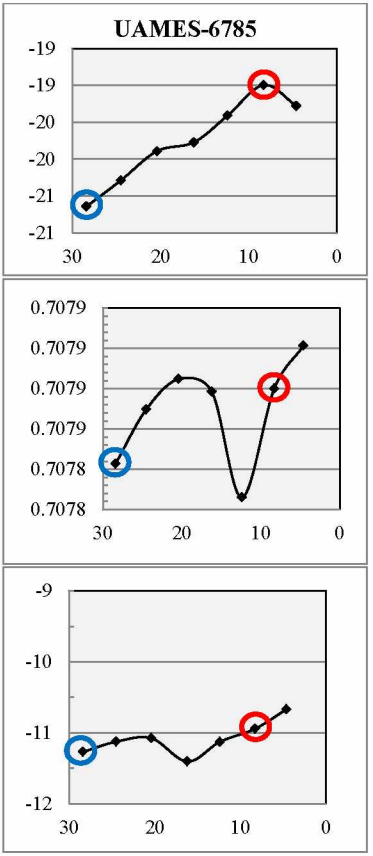

Figure 34. Individual $\delta^{18}O$, $^{87}Sr/^{86}Sr$ and $\delta^{13}C$ Graphs for UAMES-6768. Red circle indicates peak warm season; blue circle indicates peak cool season.

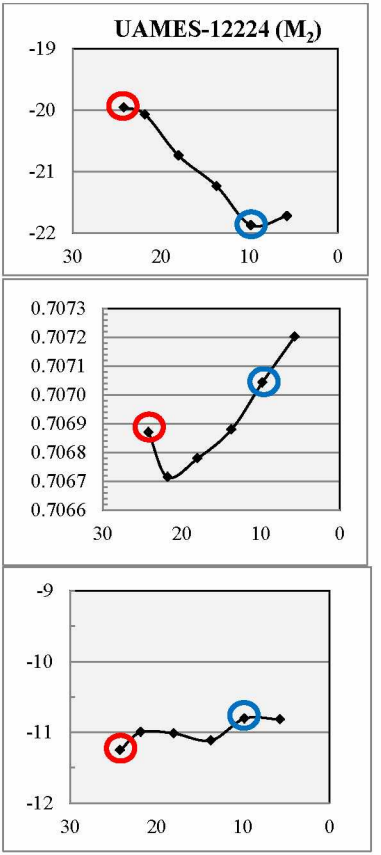

Figure 35. Individual $\delta^{18}O$, $^{87}Sr/^{86}Sr$ and $\delta^{13}C$ Graphs for UAMES-12224. Red circle indicates peak warm season; blue circle indicates peak cool season.

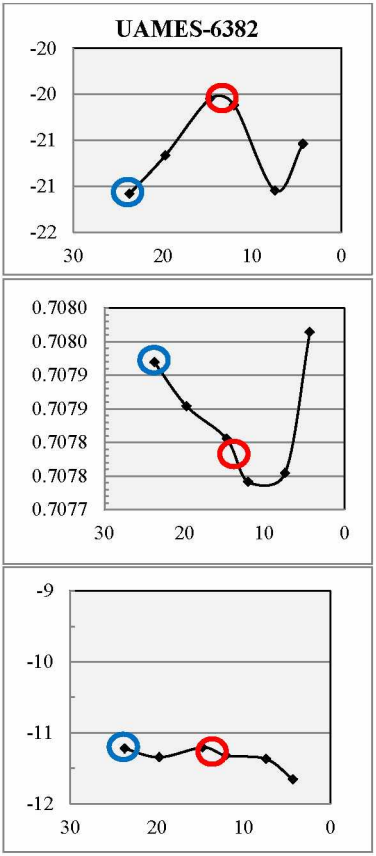

Figure 36. Individual $\delta^{18}O$, $^{87}Sr/^{86}Sr$ and $\delta^{13}C$ Graphs for UAMES-6382. Red circle indicates peak warm season; blue circle indicates peak cool season.

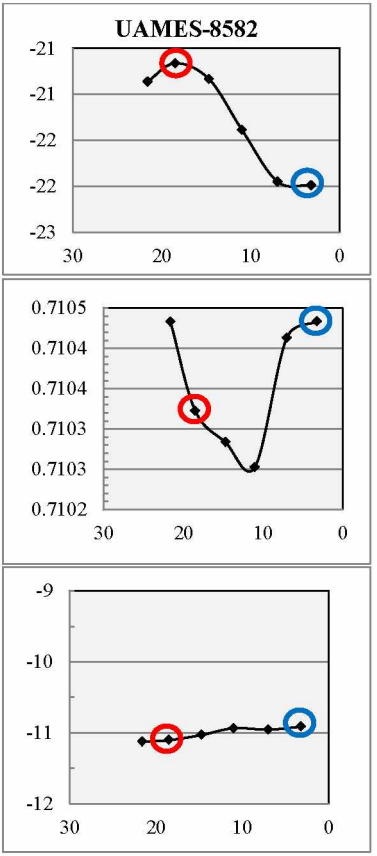

Figure 37. Individual $\delta^{18}O$, $^{87}Sr/^{86}Sr$ and $\delta^{13}C$ Graphs for UAMES-8582. Red circle indicates peak warm season; blue circle indicates peak cool season.

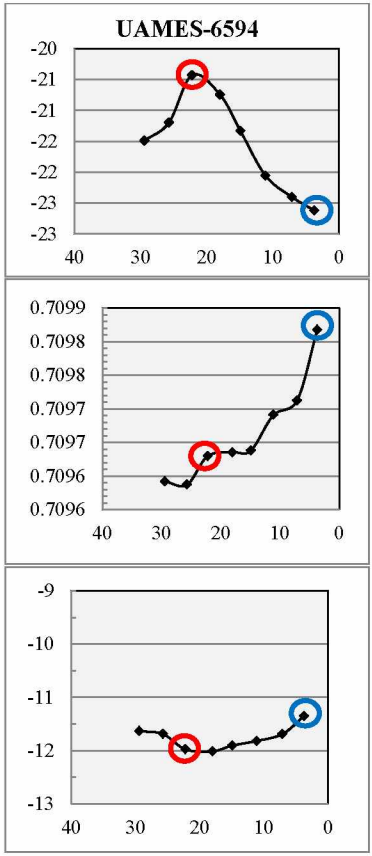

Figure 38. Individual $\delta^{18}O$, $^{87}Sr/^{86}Sr$ and $\delta^{13}C$ Graphs for UAMES-6594. Red circle indicates peak warm season; blue circle indicates peak cool season.

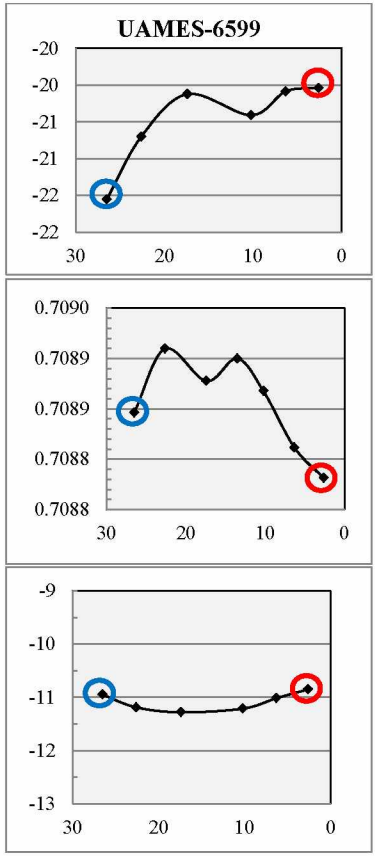

Figure 39. Individual $\delta^{18}O$, $^{87}Sr/^{86}Sr$ and $\delta^{13}C$ Graphs for UAMES-6599. Red circle indicates peak warm season; blue circle indicates peak cool season.

7.4.2 Reconstructing Environmental Context

Carbon and oxygen stable isotopes have also been used in this study to reconstruct environmental context. The sample dataset encompasses multiple climatic periods including Post-LGM Pleistocene, LGM, a warm period during the middle and end of MIS3 (locally referred to as the Fox Thermal Event; Hamilton et al. 1988), and a cooler period which occurred at the beginning of MIS3 (see Table 2 for the AMS radiocarbon results). Based on AMS radiocarbon dates, the specimens can be associated with the different climatic periods as follows:

Table 6. Association of Specimens with Pleistocene Climatic Periods

Climatic Period	Specimen ID	Age cal BP (1σ)
Post-LGM	UAMES-6335	17,060-17,680
LGM	CRREL-FPT	15,210-15,360
	UAMES-6173	20,830-21,040
	UAMES-6768	22,690-22,920
MIS3 Warm Period	UAMES-6377	31,470-31,760
	UAMES-6602	33,520-33,750
	UAMES-6620	34,600-34,860
	UAMES-6616	37,550-38,200
MIS3 Warm/Cool Transition	UAMES-6785	38,080-38,470
MIS3 Cool Period	UAMES-12224	38,430-38,720
	UAMES-6382	44,620-45,100
	UAMES-8582	46,120-46,860
	UAMES-6594	Invalid for calibration curve
>51,550 radiocarbon years BP	UAMES-6599	Invalid for calibration curve

When graphed together, there is no clear $\delta^{18}O$ pattern for the specimens, and instead a mix of different patterns are present. The modern $\delta^{18}O$ values from the Delta Bison Herd demonstrate a well-defined and predictable sinusoidal pattern (see Chapter 6) that matches expectations for modern seasonality and precipitation patterns. However, the prehistoric samples

do not all match this pattern, and instead suggest that climate and weather patterns varied during the Pleistocene. Additionally, the diversity of patterns suggests that there was variation through time in the amount and timing of precipitation, changes in when seasonal peak warm and cool seasons occurred, and variation in the intensity of seasonality and temperature extremes.

The $\delta^{18}O$ values for the prehistoric specimens follow four general patterns, displayed in Figure 40. Pattern 1 is similar to modern patterns of seasonality, and specimens UAMES-6377, UAMES-6173, UAMES-12224 CRREL-FPT, and UAMES-6785 generally match this trend, demonstrating sinusoidal waves with relatively large amplitude. This suggests that seasonal temperature and precipitation timing and distribution during the formation period for those individuals was similar to modern patterns. Specimens UAMES-6335 and UAMES-6602 have a bi-modal warm-season distribution and this is illustrated in Pattern 2. This same pattern has also been noted in time-attenuation studies measuring $\delta^{18}O$ in modern horse and bison teeth in temperate environments (Higgins and MacFadden 2004), and can be an indication of an extended period of heavy rainfall during the summer which lowers the $\delta^{18}O$ values. Pattern 3, demonstrated by specimens UAMES-6620, UAMES-8582, and UAMES-6594, has warm season peaks that demonstrate left-hand skew, with a sharp increase in values prior to the peak warm season, and a slow decrease in values after the peak warm season. Additionally, the peak $\delta^{18}O$ values occur much earlier in the sequence than in the modern specimens. This suggests that the warmest period during when those individuals were alive occurred about 2-3 months earlier than modern summers, and was accompanied by a rapid increase in temperature, before slowly cooling off. Finally, Pattern 4 is the most variable, demonstrating stepped-patterns and no discernable peak/troughs in $\delta^{18}O$ values; specimens UAMES-6616, UAMES-6768, UAMES-6382, and UAMES-6599 display this pattern. The general trend in $\delta^{18}O$ values for UAMES-

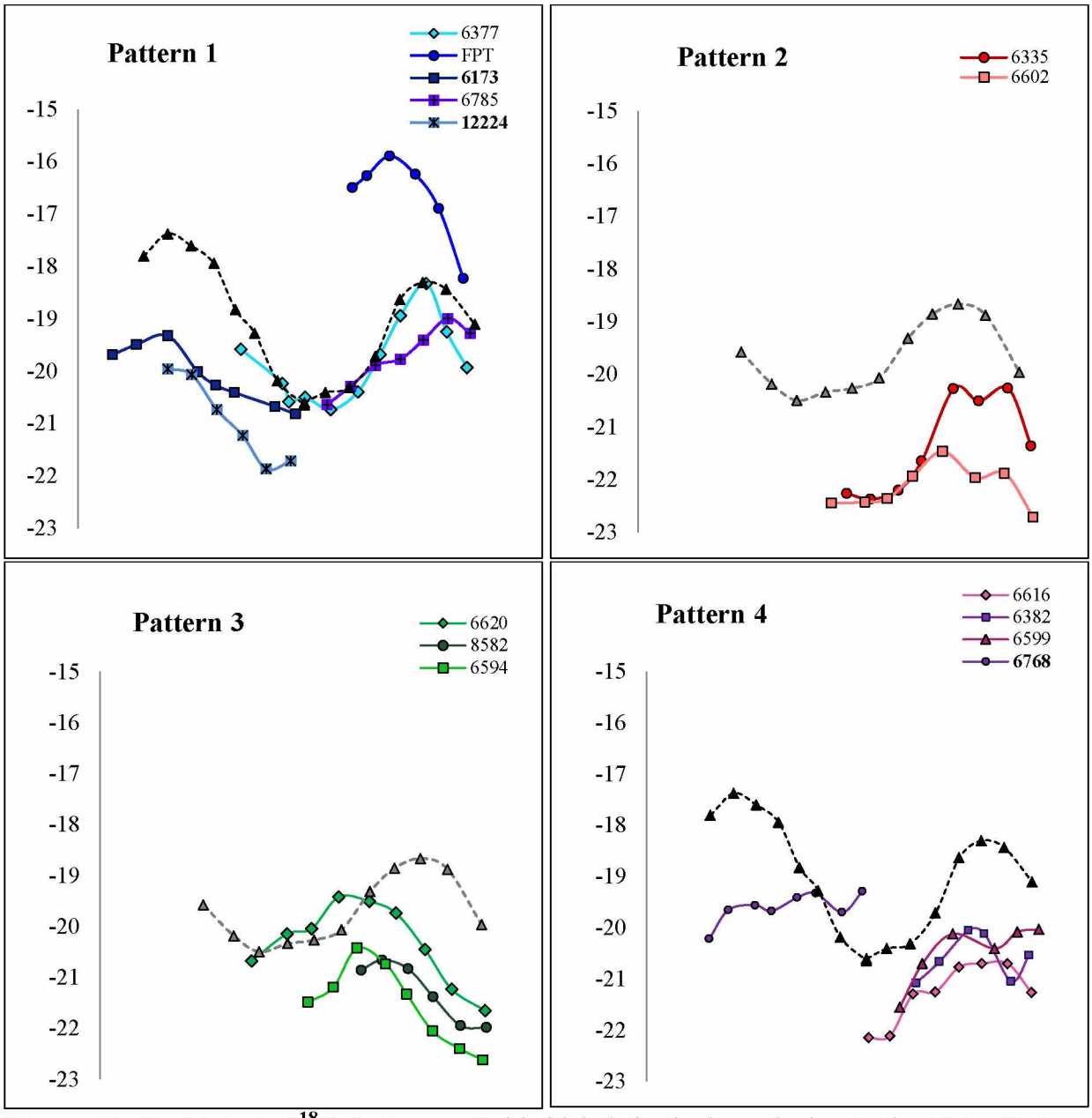

Figure 40. Prehistoric $\delta^{18}O$ Patterns. Bolded labels in the legends denote the M_2's. Pattern 1 displays similarity to modern patterns, while Patterns 2, 3, and 4 show variable trends. The black dashed line and triangular markers in Pattern 1 and 4 represent modern specimens DH1a (M_2) and DH1b (M_3). The grey dashed line and triangular markers in Patterns 2 and 3 represent modern specimen DH2 (M_3).

6768 and UAMES-6382 suggests relatively homogenous yearly precipitation and temperature, with only slight temperature increases during summer, possibly accompanied by heavy rainfall. The stepped-pattern displayed by UAMES-6616 and UAMES-6599 also suggests relatively homogenous temperature and precipitation patterns, but with slight changes that occur quickly but are homogenous for a few months, and then change quickly again and remain homogenous for another few months. While this seems to demonstrate a wide variation in weather patterns, there is no correlation between the different patterns and different climatic periods.

7.4.3 Temporal Trends in Isotope Values

This study encompasses multiple climatic periods which provides the opportunity to examine behavioral changes through time. Research on modern ungulate behavioral ecology indicates that movement can be based on many factors including forage availability, precipitation, climate, elevation, season, the presence of biting insects and predators, and physical relief (e.g., Plumb et al. 2014). Previous studies that have reconstructed bison behavioral ecology though isotopic analyses have focused on constrained temporal periods which has provided a larger quantity of data for a specific period, but has not addressed change over long periods of time (e.g., Britton et al. 2011; Julien et al. 2012; Widga et al. 2010). This method is especially useful for reconstructing factors that may have affected individual archaeological sites or periods, but does not provide a picture of long-term changes in animal behavior, or provide the means to associate behavioral changes with environmental changes. The dataset used in this study is well suited to address change over time in mobility pattern as it encompasses specimens dating to between 46,860 – 15,200 BP (and older; specimen UAMES-6594 is too old to be calibrated and UAMES-6599 dates to >51,550 BP).

One marked pattern emerges when the normalized $^{87}Sr/^{86}Sr$ values for each specimen are graphed chronologically (see Figure 41). The magnitude of variation is much greater among specimens dating to the warmer phases of the Post-LGM and MIS3 Warm Period than those deriving from cooler phases (i.e., LGM and MIS3 Cool Period). During the warmer periods, the mean magnitude of the normalized values is 0.00112, while the mean magnitude of normalized values for cooler periods is 0.00021. To determine if the difference between these two periods was significant, a two-tailed Students T-Test, assuming unequal variance was conducted. The resulting p value was 0.00000006 and demonstrated a significant difference at the 0.05 α level. This suggests that bison were significantly more mobile during warmer and wetter periods;

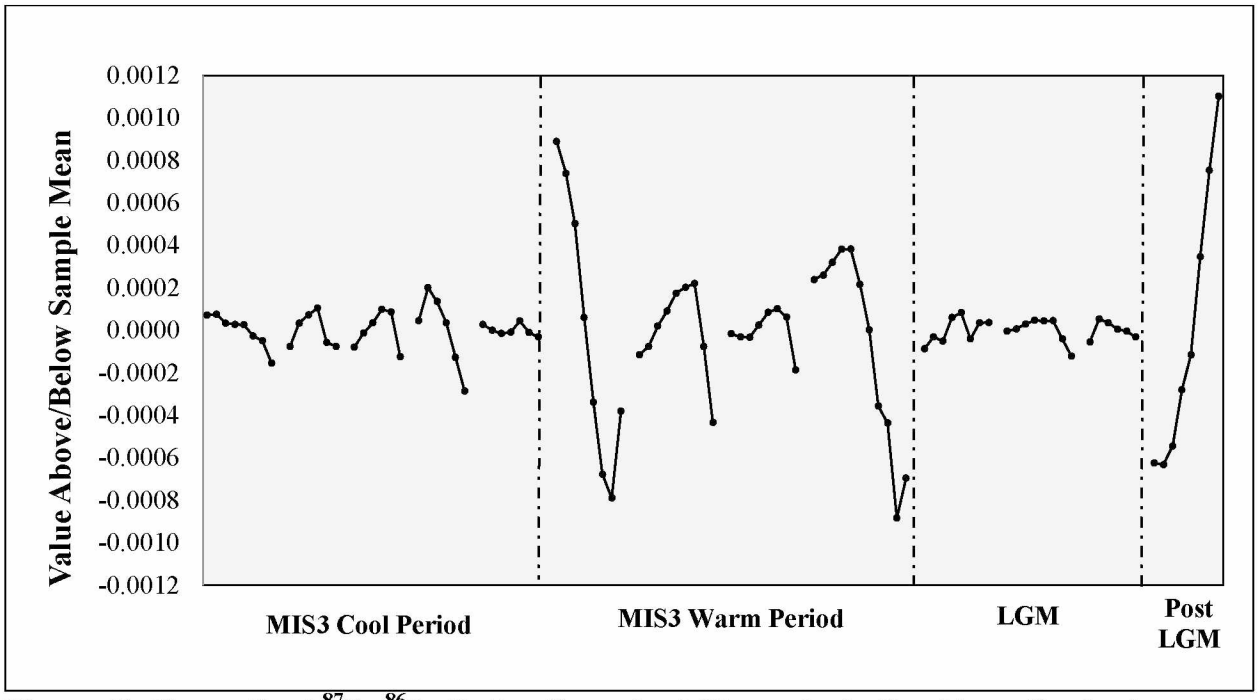

Figure 41. Normalized $^{87}Sr/^{86}Sr$ Ratios Organized Chronologically. Normalized values were determined as the difference between the specimen mean and the sample value. Specimen UAMES-6599 was not included in this graph because it could not be associated with any of the temporal periods.

however, even for the specimen with the greatest magnitude in normalized values (UAMES-6336: 0.00173) there are relatively small regions (<150 km^2) around LCC that contain the variability in $^{87}Sr/^{86}Sr$ values demonstrated by that specimen. This study has demonstrated that there is a significantly greater magnitude in $^{87}Sr/^{86}Sr$ values during warmer periods, providing a strong indication that changes in migration may be related to changes in bison migratory behavior.

7.5 Study Limitations

There are limitations to this study. First, all of the bison specimens were recovered from upland locations. As such, it is not surprising that reconstructions of their location on the landscape indicate association with upland mountainous regions. It is difficult to determine whether upland locations provided a majority of habitat area, or whether this is simply a product of the dataset (although paleontological deposits in lowland locations certainly suggests equal use of lowland regions by steppe bison [e.g., Guthrie 1968]). In order to fully understand steppe bison landuse patterns during the Pleistocene and Holocene, it would be necessary to also incorporate specimens from lowland locales, such as the Tanana or Yukon Basin. Second, only one of the specimens (UAMES-6335) overlaps with evidence for human presence on the landscape; yet, this study emphasizes that modern bison behavior is structured by environmental constraints, and their behavior should be evaluated in context of different climatic periods. Future work incorporating specimens from the Holocene will be important for further testing the ideas developed here.

However, there are two factors that suggest that this dataset is a valid source of information for bison behavior in the Late Pleistocene and Holocene (and hence, valid for

modeling human behavioral responses as well). First, the dataset includes several specimens dating to the MIS3 warm period (between ~36,000-30,000 BP), which is thought to be similar to post-LGM Pleistocene and Early Holocene climates (e.g., Anderson and Lozhkin 2001). During both of these periods of ameliorated climate there was a spread of mesic-adapted shrub tundra and an inferred rise in birch and populous vegetation (e.g., Anderson and Lozhkin 2001; Hopkins et al. 1981; Wooller et al. 2007). While there certainly were differences between these two periods (most notably that the Pleistocene-Holocene transition occurred rapidly and on a larger scale), these two periods do have broad environmental similarities in climate and vegetation. These similarities are also illustrated in the dataset, and specimens dating to the climatically-warmer periods have similar magnitude of variation in the $^{87}Sr/^{86}Sr$ ratios.

Second, this dataset encompasses ~35,000 years, and throughout the entire sequence, there are similar patterns in seasonal behavior. Regardless of time period, the dataset indicates that bison were mobile on a seasonal basis, and demonstrates migration between upland ecotones during the summer and lowland ecotones during the winter. While this pattern cannot be inherently assumed for Holocene bison populations, the results are strongly indicative that this pattern was the dominant seasonal behavior for this species for over 35,000 years (and is also the same seasonal pattern demonstrated by modern bison populations [*c.f.,* Grogan et al. 2010; Meagher 1973]). There is little reason to expect that this pattern would have changed during the Holocene, and it is assumed that this seasonal pattern of migration would have continued. Therefore, while this dataset is limited to specimens from upland locations, and while only one specimen that coincides with the period of initial human occupation, it can be argued that this dataset provides reliable information for characterizing human reliance on bison as a subsistence resource during both the Late Pleistocene and Early Holocene.

7.6 Summary

The results of this study demonstrate a number of informative patterns in $^{87}Sr/^{86}Sr$, $\delta^{18}O$ and $\delta^{13}C$ values. The 14 specimens used in this study were well preserved, and with the exception of one sample (the 4th sample removed from specimen UAMES-6599), are assumed to provide accurate isotopic signatures. Collectively, the $^{87}Sr/^{86}Sr$ and $\delta^{18}O$ results suggest that steppe bison were seasonally migratory, likely moving between higher elevation locations in the summer and lower elevation locations in the winter, and showed association with larger upland river valleys and basins in the YTU. There was also significantly greater mobility during the Post-LGM and MIS3 warm period which are associated with more mesic conditions; however, the variability in $^{87}Sr/^{86}Sr$ values for all periods and specimens can be encompassed within relatively small regions and migration could have occurred on a relatively small scale. As previous research has indicated, the $\delta^{13}C$ results show that bison were consuming graminaceious vegetation (e.g., Fox-Dobbs et al. 2008; Guthrie 1990; Rivals et al. 2007, 2010; Wooller et al. 2007), and changes in the values through time match expectations for changes in temperature and precipitation. The $\delta^{18}O$ results indicate that climate during the Pleistocene was highly variable in terms of seasonal temperature variation and precipitation, although further research is needed to fully understand these patterns. These results contribute to a greater understanding of animal behavior both from an ecological and archaeological perspective, and are discussed more fully in the following chapter.

CHAPTER 8: MODELING THE HUMAN-BISON RELATIONSHIP

As discussed in the previous chapter, the results of this study indicate that bison moved small distances (<700 km^2) seasonally, likely spending summers in higher elevation regions and winters in lower elevation regions. Additionally, the individual specimens in this study demonstrate $^{87}Sr/^{86}Sr$ patterns that suggest association with large river basins in upland[9] locations in the YTU, which may have provided seasonal habitat area during winter. This chapter considers the broader implications of this data in terms of how this may have affected human populations during the Late Pleistocene and Early Holocene.

8.1 Seasonal Model of Bison Predictability and Availability

The archaeological record of the Tanana Valley indicates that bison were a large component of subsistence economies during the Late Pleistocene and Early Holocene. However, this does not imply that prehistoric groups were bison specialists. Rather, the faunal record indicates that diets during that period were relatively broad-spectrum and incorporated a variety of large and small game, as well as waterfowl, fish, and plant resources (e.g., Holmes 2011; Potter 2005; Potter et al. 2011, 2013a-b, 2014; Yesner 1996, 2001; Yesner et al. 2011). However, because bison (and wapiti) were the largest bodied game species they would have contributed to a larger proportion of the diet than small game or other seasonally-available resources.

HBE models (discussed in Chapter 3) generate the expectations that the most productive food sources would be harvested and consumed first, and lower-ranking food sources would only

[9] "Upland" locations are defined as per Gallant et al. (1995:1): a discontinuous ecoregion of "rounded, low mountains often surmounted by rugged peaks".

be added to the diet during adverse conditions (i.e., MacArthur and Pianka 1966). Because bison would have been the highest-ranking resource, they therefore should have been selected for and sought out on the landscape until that resource patch began to decline (i.e., Charnov 1976; Smith 1983). Based on these optimal foraging perspectives, bison seasonal movement patterns and behavioral ecology likely would have constrained human settlement and subsistence patterns to some degree.

Chapter 3 discussed two general models for how bison seasonal behavior could have affected human behavior. The first model predicts that if bison were seasonally migratory on a large scale (i.e., migrating hundreds of kilometers throughout the year), then subsistence and settlement patterns would have likely been organized around logistical mobility. Bison would have represented a seasonal food-source, and bison hunting would have likely incorporated organized logistical forays specifically targeting bison as they moved through certain regions on their annual migration. The second model predicts that if bison did not migrate seasonally (or only migrated short distances [on the order of <700 kilometers per year]), then bison hunting could have occurred during any season, and rather than specific hunting events as the bison passed through the region during certain periods. Under the non-migratory model, bison would have represented a predictable food source that was available throughout the year, and would have represented a mainstay food source that was supplemented by other seasonally available food source such as plants, small game, and migratory waterfowl.

As discussed in Chapter 7, the results of this study suggest that bison were seasonally migratory, but on a relatively small scale (i.e., migrated <700 kilometers/year). This suggests that settlement patterns may have been broadly organized around residential mobility during the Late Pleistocene and Early Holocene, at least during certain times of the year. However, as

Kelly and Todd (1988) suggested, both logistical and residential mobility may have been operating in settlement systems during the Late Pleistocene and Early Holocene. Certain animals, such as bison or wapiti, may have been targeted through more logistical hunting forays, while small game and plants may have been procured on an encounter basis (Kelly and Todd 1988).

Because of the likelihood of multiple settlement patterns operating at once, and the fact that human settlement and subsistence behavior is highly variable and would have been constantly changing in concert with seasons, weather, resource availability, social dynamics and myriad other factors (*c.f.,* Kelly 2013), seasonal models of optimal behavior in regards to bison procurement are discussed in the following sections. These seasonal models incorporate the results of this study, information from the ethnographic record from both Athabaskan and Plains groups, and information about modern bison herd population dynamics. This ethnographic information is not intended to be used as a direct analog for prehistoric human behavior, but rather as a broad framework to conceptualize human behavioral responses and subsistence and settlement organization. Along the same vein, the data on modern bison are not meant to provide a direct analog for prehistoric extinct bison species, but rather a basis for understanding how bison behavior may have been broadly organized or constrained based on environmental influences, and when bison likely would have been the most predictable[10]. Table 7 provides a matrix of bison seasonal behavioral dynamics, and combines the results of this study with the information on modern bison herd behavior (discussed in Chapter 3). Table 7 is discussed more fully in the following sections.

[10] High bison predictability is defined as periods throughout the year when bison occurred at certain places on the landscape and were aggregated into large groups during certain times of the year. High predictability would mean a high success rate of bison harvest, but only if they were specifically targeted. As such, low predictability implies that bison would be dispersed and more likely harvested on an encounter-basis rather than through logistical forays.

Table 7. Bison Seasonal Behavioral Dynamics and Predictability

	Herd Social Structure	Dispersal Pattern	Physiographic Location	Patch Duration	Encounter Rate	Nutritional Quality	Seasonal Resource Competition
WINTER	Variable; females and juvenile males most common	Variable	Lowland river valleys	5-6 Months	Variable	Low	None
SPRING	Females, calves, and juvenile males	Large calving herd + solitary bachelor bands	Transitioning to upland locations	4-6 Weeks	Highest	Lowest	Migratory waterfowl, caribou
SUMMER	Females, calves, and juvenile males	Small bands of ~dozen individuals (?)	Uplands	2-4 Months	High in upland locations	High	Migratory waterfowl, plants, salmon
FALL (RUT)	Males and females of all ages	Largest herd: all individuals	Uplands (?)	6-8 Weeks	Highest	Highest	Migratory waterfowl, caribou, berries

8.1.1 Winter

Winter is the riskiest season in the north, and having predictable sources of food and shelter is essential. The ethnographic record indicates that for Athabaskan groups, food caches that had been built up over the summer and fall were exhausted by January, and settlement was dispersed into one or two nuclear families living in portable skin shelters (McKennan 1959; Osgood 1936). During the peak of winter, lowland[11] regions offered the most variety and

[11] "Lowland" locations are defined as per Gallant et al. (1995:1): an ecoregion of "flat to nearly flat bottomlands along larger rivers of interior Alaska…[and] dotted with thaw and oxbow lakes".

predictability of resources, including fur-bearers which were essential for clothing and large-bodied ungulates that were dispersed in willow thickets in valley bottoms (West 1963).

The results of this study indicate that bison spent winters at lower elevation areas, likely relying upon the more productive and nutritious riparian zones in river valleys. Data on modern bison herds suggests that creek bottoms and sloughs were used for grazing during the winter due to those locations having a higher plant nutrient composition than other areas (Reynolds et al. 1978). Additional support of this winter behavioral model is found in the $\delta^{13}C$ data in this study, which shows a slight increase in values for many of the specimens during the peak cold season. This slight increase may signal a change in foraging behavior during those periods. Wood bison typically graze on lowland meadow or forest vegetation during the winter and as forage quality begins to decline in the fall, bison begin using a wider variety of habitats and begin consuming large quantities of lichens (Later and Gates 1991). Research by Rivals et al. (2007) suggest that for a least a portion of the year, steppe bison consumed woody vegetation, which further suggests the use of more vegetated valleys during the winter.

The dispersal pattern of the herds may have been variable during winter, as predators, food availability, snowfall, and other factors can constrain herd behavior (see Chapter 3). In mountainous regions, modern bison form small herds of 15-20 individuals throughout the year, and typically do not form larger herds except during the fall rut (Hess 2002). It is possible that small 'patches' of similarly-sized bison herds would have occurred throughout river valleys and basins for 5-6 months of the year during the Pleistocene and Early Holocene.

In one aspect bison herds would have likely been limited to valley bottoms, making them somewhat of a reliable winter resource in terms of where they were located on the landscape; however, they likely were spread out into small groups that may have been difficult to target

through logistical hunting, making them somewhat of an unpredictable resource, similar to moose. Hunting on an encounter basis may have been the most productive for harvesting bison in the winter, although this may have been variable based on environmental variability from year-to-year. Additionally, while bison are not as nutritionally-rich during the winter as other seasons (*c.f.,* Guthrie 1982a), they still would have represented the highest-ranking resource (along with wapiti) during the Late Pleistocene and Early Holocene, likely making them a primary resource during winter months.

8.1.2 Spring

Spring was known as the starvation time for Athabascan peoples as resource caches from the previous year were depleted and seasonal migrations of game resources not yet begun (e.g., McKennan 1959; Osgood 1936; West 1963), and this may have been the case for prehistoric groups as well. During the spring animals are at the most lean point of the year with very little body-fat reserves (*c.f.,* Guthrie 1982a), which makes them a nutritionally-depleted and unpredictable resource. However, after break up, migratory waterfowl begin to return and large ungulates would have begun to have calves, thus increasing the overall resource predictability and availability on the landscape.

While the current dataset does not inform on steppe bison population density, information from modern herds suggests that bison are widely dispersed in spring and do not begin to aggregate into larger herds until calving season (Plumb et al. 2014). While there was still snow on the ground, steppe bison may have been spread out into small groups (a dozen individuals) through larger river valleys and productive riparian zones where there was still some available forage. Snow depth and predator density likely impacted their aggregation behavior from year to

year however. Deeper snow, especially in spring, may have forced them to be more dispersed in order to find forage; conversely, predation pressure may have forced them to congregate in larger numbers (see Chapter 3). This general pattern of dispersion throughout river valleys would have likely been similar for other large ungulates such as caribou and wapiti (e.g., Jakimchuk et al. 1987; McCorquodale 2003).

Similar to winter, the predictability and dispersion of bison was likely variable in the early spring. If forage was scarce, the herds would be the most scattered compared to other times of the year. However, if there was deep snow or an abundance of predators, the bison may have been aggregated into larger groups. The results of this study indicate that bison spent summers in upland locations, and migration to summer habitat areas likely occurred soon after plants began growing.

For bison, calving season may have caused them to congregate into matriarchal bands in upland south-facing locations where visibility was good for keeping a predator lookout, where there was escape from biting insects, and where there was a supply of fresh greens for essential nutrients after the long winter (e.g., similar to the Delta herd [Chapter 6] and bison in Yellowstone [Meagher 1973]). Calving season lasts ~4-6 weeks for modern bison, and the female-calf pairs and other yearlings typically stay relatively close together during this period (see Chapter 3). Late spring likely would have brought greater predictability in terms of where they were located on the landscape, and during this period (especially if other resources were scarce) bison may have been targeted as a much-needed resource after the winter.

8.1.3 Summer

As opposed to spring, an abundance of resources would have been available during summer. Summer (and early fall) would have been the only time to gather plants for use as food, medicine, and raw material. Ethnographic information indicates that large mammals were not as heavily relied upon for food during this season although they were still harvested on an encounter-basis (McKennan 1959; Osgood 1936). For Athabascan peoples, fish, small game, and plants comprised a large portion of summer diets (McKennan 1959). While the resource base during the Late Pleistocene and Early Holocene was much different than during the Athabaskan period, there is still evidence that summer diets incorporated a wide variety of resources including small game, fish, and plants (e.g., Potter et al. 2011).

The results of this study indicate that bison migrated to higher elevation during the warm season. Bison likely spent summers in mountainous foothills where they could consume highly nutritious summer forage. The herds were likely spread out into matriarchal bands between 12-50 individuals during the summer (see Chapter 3) and would have been spread out across the foothills at similar altitudes. For modern bison, dust wallows are important in the summer for protection from biting insects (e.g., Plumb et al. 2014), and the more xeric conditions of south-facing slopes may have provided excellent conditions for dust wallows. In addition, high elevation ice-patches may have also been an appealing refuge from insects and summer heat. Modern caribou seek high elevation ice-patches during the summer as did prehistoric caribou populations (e.g., Farnell et al. 2004), and ethnographic accounts also describe hunting caribou during the summer at high elevation locations near ice-patches (*c.f.,* Hare et al. 2004).

A wide-spectrum of resources would have been the most available and predictable during summer months than during any other period of the year. The modern summer growing season

in Alaska lasts for ~2-4 months and likely lasted for a similar duration during the Late Pleistocene and Early Holocene. The location of bison may have been somewhat unpredictable during the summer however, as they may have ranged over a large expanse of upland areas during the summer months. Regardless of the degree of predictability however, reliance on bison as a key resource (and the harvesting of more than a few lone individuals on an encounter-basis) would have necessitated being in upland locations during the summer.

8.1.4 Fall

For Athabaskan groups, fall was a period of intense activity in preparation for winter by gathering and caching food stores, trapping fur-bearing animals for winter clothing, and gathering lithic and organic materials for tools and implements; people would also migrate to upland areas in anticipation of seasonal caribou migrations. Caribou fences were used to harvest dozens of animals at a time and required the participation of many families, and if the harvest was good, families would stay in those regions for several months (McKennan 1959; Osgood 1936; West 1963).

Data on modern bison herds suggest that fall is the most predictable season for hunting as this is when the largest herds aggregate in localized regions (Berger and Cunningham 1994; Lott 1981; Olson 2005; Plumb et al. 2014). Presumably, steppe bison would have also congregated in restricted locations in upland foothills during the fall for mating season that would have lasted 6-8 weeks (see Chapter 3). However, as Olson (2005) noted, the aggregation of a rutting herd requires a lot of forage, and modern herds move about during this period, but do not cover long distances, suggesting that they would have been located in a relatively predictable location on the landscape during rutting season.

This large and predictable aggregation (both in terms of timing, location, and number of animals) would suggest that bison, along with other large ungulates, would have been intensely hunted during the fall. During the fall (and in particular during the rut), bison may have been harvested through logistically organized forays targeted at procuring multiple individuals at once. The bones, horn and hides could have been processed for clothing, shelter, and tools, and the meat could have been cured for storage (or made into pemmican (*c.f.,* Guthrie 1982a; Kelly and Todd 1988). However, bison likely represented only one component of a broad resource strategy, and during the fall, migratory waterfowl, seasonally-available berries and plants, and other resources would have been intensively harvested, suggesting that multiple subsistence strategies may have operated simultaneously. This model of the various seasonal bison behavior and resource availability is discussed with regards to how it would have specifically affected human behavior in the following section.

8.2 Modeling Human Settlement and Subsistence Patterns

Reconstructions of the mobility patterns and behavioral ecology of high-ranked faunal resources can have important implications for reconstructing and understanding prehistoric human behavior, especially for foraging and collecting populations (e.g., Britton 2009; Frison 2004; Rivals et al. 2007; Widga 2006). This is due in part to the fact that many species vary in their seasonal distribution, predictability of behavior, and population densities. Furthermore, if any of these factors change, over either the short-term or long-term, this can have marked implications as to how humans may alter their seasonal behavior.

Binford's (1980, 2001) discussion of residential vs. logistical mobility is especially informative for understanding site patterning and human behavior in the archaeological record.

However, human settlement and mobility patterns are constrained by resource predictability and availability on the landscape (*c.f.,* Kelly 2013). When there is homogenous resource distribution, foraging is typically the main subsistence structure, but when there is a high degree of resource patchiness or unpredictability, collecting is typically the subsistence structure (Binford 1980, 2001). Both residential and logistical mobility can incorporate high degrees of mobility; however, dependence on large-bodied game is typically associated with heightened mobility (Kelly 2013). Kelly and Todd's (1988) model of Paleoindian hunting and mobility patterns during the Late Pleistocene and Early Holocene also emphasize very high rates of mobility, as well as reliance on large game. These factors set up some key expectations about how settlement patterns may have changed on a seasonal basis.

8.2.1 Human Seasonal Landuse

Prehistoric human groups in interior Alaska would have been highly mobile throughout the year, regardless of settlement and subsistence organization. Because these populations relied on bison as a key component of the subsistence economy, there may be broad trends in the probability of seasonal site location. Bison would have been most predictable and readily available during the winter and early spring in lowland areas, and during the summer and fall the most predictable and available in upland areas. Late spring, summer, and fall logistical hunting camps should be expected in upland locations, while residential base camps may have either remained in lowland locations or may have been moved areas adjacent to multiple ecotones in order to exploit the widest range of resources during these seasons. Winter sites were likely located in lower elevation regions, with a higher probability of winter residential sites occurring peripherally to productive riverine ecotones where there would have been the largest densities of

large ungulates. This prediction of seasonal site locations is supported by much of the archaeological record for the region, and Potter (2008a, 2011) noted a division the lithic technology between upland and lowland areas, suggesting that early subsistence economies incorporated both regions, and similarly, Wygal (2011) suggested that use of upland and lowland areas may have been organized seasonally around the exploitation of different species.

For the study region, the results suggest that landforms adjacent to Mosquito Flats, the Mosquito Fork River, and the Dennison Forks of the Fortymile River provided habitat for bison populations, and this region may contain Late Pleistocene and Early Holocene winter residential and hunting camps. Additionally, low-elevation riparian zones along the northern portion of the Tanana River Valley likely provided bison habitat, and landforms along this region may provide a higher probability for locating winter encampments. It is interesting that the Delta bison herd (even prior to human influence on their mobility patterns) favors a north-south seasonal migration route, spending winters to the north along the lower protected regions along the Tanana River adjacent to the YTU, and summers to the south in the more recently glaciated foothills of the Alaska Range (see Chapter 6). This pattern may have also been reflected in prehistoric seasonal bison habitat use as well.

In addition to general seasonal patterns of upland vs. lowland site distribution, there were also changes in the predictability and distribution of prey species on a seasonal basis that likely constrained human settlement and subsistence patterns in other ways. Spring would have represented the riskiest time with the greatest unpredictability in the availability, distribution, and nutrient content of animal resources, and limited plant resources. Bison and other large game populations likely were the most dispersed in spring, which would have necessitated a more

mobile subsistence pattern, likely reflected in greater residential mobility and a dispersion of single family groups across the landscape.

Summer would have been the ideal time for more logistically organized behavior. A division of labor with small dispersed groups logistically-organized around a central residence would have allowed for the collection of the greatest diversity of food and material resources. Population density at single sites may have increased as multiple family groups joined together after dispersing during the lean times of late winter. As mentioned previously, residential camps were likely located at the edges of different ecozones in order to collect the greatest variety of resources. Component 3 at Upward Sun River is the best example of how a summer residential camp might have functioned (Potter et al. 2011, 2014). The faunal evidence suggests that small game, fish, plants, and water fowl were harvested from the immediate vicinity, while groups of a few individuals likely ranged out and gathered other resources from more distant patches which would have been brought back to the residential base. Additionally, there is evidence of a semi-subterranean structure as well as indoor and outdoor activity areas at the site (Potter et al. 2011) suggesting longer-term occupation. Notably, there is also evidence for ideological belief-systems and potential gender and age-based social structures as well (Potter et al. 2014), providing a more throughout picture of lifeways during the Late Pleistocene and Early Holocene than ever before.

Other sites in the Tanana Valley seem to have been occupied as residential camps during the warm season, including Broken Mammoth CZ4 (~13,500 BP) and Mead CZ4 (~12,900 BP) and CZ3b (~12,000 BP) (e.g. Krasinski and Yesner 2008; Potter et al. 2011, 2013a, 2013b; Yesner 1996, 2001). Throughout all of these components, there is faunal evidence for a wide spectrum diet, including an abundance of small game and waterfowl as well as high utility

elements of large game (e.g. Potter et al. 2013a). This fits the expectation that a wide range of resources would be present at residential camps as small game would be harvested from the immediate vicinity, and the high-utility portions of larger game would be brought back from hunting camps located a few days away. Additional evidence that suggests these components were residential bases includes spatial patterning indicative of specific activity areas, arcs of debris which suggest the presence of residential structures (Potter et al. 2013b), and evidence of organic implements being produced and used (Yesner 2001).

In fall, steppe bison likely congregated into large herds during rutting season for about 6-8 weeks, and this would have presented one of the best opportunities for harvesting multiple animals at one time. Fall necessitated preparation for winter. Large game was likely hunted via logistically organized and task-specific hunting camps where the meat was processed before being transported back to the residential camp and cured for winter use. The short term hunting camp at Component 3 at Gerstle River provides a potential example of this type of hunting and processing camp where high utility elements were likely transported back to a residential camp (Potter 2005, 2007). Broken Mammoth CZ3 (~12,050 BP) has been interpreted as a fall occupation, and at least 73% of the identified faunal specimens from that component are from bison (Potter et al. 2013b), suggesting that bison were intensively harvested from nearby areas during this occupation. Two uplands sites that have been interpreted as having fall components and that focused on big-game hunting include Dry Creek and Carlo Creek in the Nenana River Valley. Component 1, (~11,400 BP) at Dry Creek has been interpreted as a fall camp of relatively short duration where bison, wapiti, and sheep were hunted (Powers et al. 1982; Powers and Hoffecker 1989). Nearby Carlo Creek Component 1 (~11,300 BP) has also been interpreted

as a short-duration hunting camp where caribou, Dall sheep, and ground squirrel where processed (Bowers 1980; Bowers and Reuther 2008).

Together, this information from both lowland and upland components provides an indication that large-bodied ungulates were actively sought out in the fall, likely in preparation for winter. It is likely that resource collection was specific, targeted, and highly organized in the fall. A portion of the group may have remained at a centrally-located residential camp to cure and store food, sew clothing, mend shelters, and make the necessary tools and implements for the imminent winter, while small groups a few individuals ranged away from the camp for coordinated specialized tasks. A bone needle was found in Broken Mammoth CZ4, and along with a diversity of game species (Yesner 2001), this may indicate that this site functioned as a late summer or fall residential camp where clothing and shelter may have been sewed or mended, and a variety of food sources may have been stockpiled in preparation for winter.

Duration of fall residential base camps would have been dependent on the density of nearby plant and animal species, but if bison herds were aggregated for several weeks at a time for the fall rut, human encampments may have been occupied for a similar duration as well. Guthrie (1982) suggested that more permanent fall camps would have allowed small groups to forage greater distances and add to a greater variety of winter stores. However, as the bison would begin to disperse post-rut, they would become relatively less predictable, and hunting them would have required increased human mobility and dispersion. This was likely reflected in the settlement and subsistence patterns which may have transitioned from large and longer-duration fall residential camps where resource gathering was logistically-organized, to smaller camps that were occupied for a shorter-duration and moved more frequently during the winter.

8.3 Temporal Changes

There appears to have been a significant increase in bison mobility during climatically-warmer periods when woody vegetation increased and spread across portions of the landscape. Guthrie (1982) hypothesized that as climates warmed at the end of the Holocene, changes in the vegetation mosaic would have partitioned bison habitat which would have split up the herds and forced them to condense into smaller portions of the landscape. As woody vegetation increased, this fragmentation in habitat would have created a barrier and cut off gene-flow between different populations. This, coupled with lack of forage and habitat encroachment, may have been the primary factors that caused steppe bison to eventually become extinct in Beringia. These hypotheses have been suggested for decades (e.g., Zimov et al. 1995), but this study reflects one of the first empirical datasets to indicate changes in mobility patterns over time.

8.3.1 Changes in Bison Habitat and Behavior

The inclusion of steppe bison specimens from lowland locations would be necessary to definitively speak to the availability of upland vs. lowland habitat; however, this initial dataset suggests that upland mountainous locations provided important bison habitat during the last 35,000 years of the Pleistocene. Work by Dilley (1998), Reuther (2013) and others have indicated that throughout the end of the Pleistocene, the landscape of interior Alaska was much more active than at present, with katabatic winds sweeping off of the glaciated portions of the Alaska Range, forming shifting dune fields and depositing meters of loess throughout the southern foothills of the YTU. It is possible that during the height of glacial periods, upland regions provided refugia from the blowing sheets of sand and loess that swept through lowland

valleys, and supported the growth of forage and habitat area for steppe bison and other megafaunal species.

As the environment became less active at the close of the Pleistocene, regions that were once too harsh for animal populations appear to have stabilized, and these became favored habitat locations for bison and wapiti (*c.f.,* Reuther 2013). There seems to have been a florescence of ideal big-game habitat throughout the Tanana River Valley at the close of the Pleistocene (e.g., Guthrie 2001, 2006), but this did not last. As the landscape stabilized at the end of the Younger Dryas, the spread of woody vegetation likely decreased habitat availability and forced bison herds to fragment into smaller and smaller populations which had to move greater distances to find seasonal habitat. This suggests that as the Holocene progressed, bison populations would have slowly decreased in their availability and predictability. The implications for how this would have affected seasonal human behavior are discussed in the following section.

8.3.2 Changes in Settlement and Subsistence Organization

If bison migrated farther distances during climatically-warm periods associated with the spread of woody vegetation, this may suggest that bison were less mobile during the Late Pleistocene when there was a greater availability of open habitat. As the Holocene progressed, bison may have become more mobile and dispersed as climates continued to warm and trees spread across the land. If this was indeed the case, it would suggest that bison were a more predictable resource during the Late Pleistocene, and as time passed, they would have become less and less predictable, necessitating shifts in subsistence economies to other resources. In fact, this is the pattern reflected in interior Alaskan faunal assemblages. Potter (2008b) has

indicated that there was a marked shift in subsistence patterns around 6,000 BP, and faunal assemblages around this time switch from being bison-dominated to being caribou-dominated.

Models of risk-mitigation suggest that a frequent response to decreased predictability in the environment is increased mobility. If so, this might suggest that logistical mobility structured settlement and subsistence patterns to a greater degree during the Late Pleistocene, and residential mobility structured settlement and subsistence patterns to a greater degree during the Early Holocene. Binford (1980) also noted that logistically organized groups will frequently reuse the same locations on the landscape, coming back to the same sites or features on the landscape year after year. Residentially organized groups often use different portions of the landscape on an ad-hoc basis, and do not frequently reoccupy the same portions of the landscape. Interestingly, there are multiple occupations of the same sites during the Late Pleistocene and Early Holocene such as Broken Mammoth, Mead, Swan Point, Upward Sun River, Healy Lake, and Gerstle River (*c.f.,* Potter et al. 2013b), but after about 9,000 BP, those sites are infrequently reoccupied, suggesting that landuse patterns changed on a very broad scale. One possible explanation is that there was a shift from greater logistically-organized settlement and subsistence during the Pleistocene and Early Holocene to a more residentially-mobile pattern sometime in the mid-Holocene when bison populations became increasingly fragmented and unpredictable.

8.4 Summary

To conclude, the seasonal movement patterns of bison and the general seasonal availability of other prey species has numerous implications for how prehistoric people may have structured their seasonal landuse patterns. Spring would have been the most difficult time to

procure food resources, while summer and fall would have provided both abundance and predictability of resources. Bison hunting during these periods would have likely occurred at upland locations, and settlement patterns may have reflected the Orb Model (*sensu* Guthrie 1982a) where relatively-long term residential camps would be centrally-located in regions with diverse resources, and small groups of a few individuals would range out and collect resources in spike-camps. In winter, prey species are dispersed, but likely would have been located in valleys and productive riparian zones. The data indicates that bison spent winters at relatively low elevation regions located in river valleys. This may have required increased residential mobility to obtain food resources during the winter. The data also suggests that bison mobility may have increased as climates warmed, which would have decreased their predictability as a key resource. This may have been reflected in settlement and subsistence patterns as a shift towards greater residential mobility. These models are supported by data from the archaeological record, and suggest that human landuse patterns were dynamic and adapted to seasonal, as well as long-term, ebbs and flow of resource availability.

CHAPTER 9: CONCLUSION

Steppe bison were one of the quintessential Pleistocene species. Studies in ecosystem dynamics (e.g., Knapp et al. 1999), archaeology (e.g., Potter et al. 2013b) and ethnography (e.g., Stephenson et al. 2001) suggest that bison were essential components of the ecology and human history of interior Alaska for millennia. And yet, little is known about where their primary habitat was located, how they moved about the landscape on a seasonal basis, or how their behavioral ecology may have changed in response to environmental change. Previous reconstructions of steppe bison behavioral ecology have relied heavily on actualistic models of modern bison behavior (e.g., Guthrie 1990), but there is a growing body of literature that suggests seasonal movement patterns and habitat choice are structured by a number of environmental factors (e.g., Plumb et al. 2014), and therefore, modern data may not be an adequate proxy for reconstructing the behavior of extinct bison species.

This study sought to address this void in knowledge about steppe bison seasonal behavior and movement across the landscape for interior Alaska during the Pleistocene. Four specific research questions were addressed: 1) whether steppe bison were seasonally migratory; 2) whether there were any physical features on the landscape that could be associated with steppe bison; 3) whether there were any changes over time in steppe bison mobility patterns; and finally, 4) how steppe bison behavior could have affected prehistoric human subsistence and settlement patterns.

This was accomplished by sequentially-sampling 14 bison teeth from two locales in the YTU and analyzing the individual samples for $^{87}Sr/^{86}Sr$, $\delta^{18}O$, and $\delta^{13}C$. This study relied heavily on the strontium isoscape published by Bataille et al. (2014), and it was through comparisons with the predicted $^{87}Sr/^{86}Sr$ distribution that mobility patterns were reconstructed

for the sample dataset. The results indicate that steppe bison were moving across the landscape on a seasonal basis, but were not covering large distances, and bison appear to have been moving between higher elevation regions in the summer and lower elevation regions in the winter. There also was a close association between the specimen $^{87}Sr/^{86}Sr$ values and large river basins in the YTU, specifically the southern forks of the Fortymile River. These results, along with information on modern bison behavior in high latitude and high elevation environments, suggests that bison summer habitat was located in upland regions were there was likely an abundance of highly nutritious forage, with winter habitat located in lowland regions along protected but highly productive riverine ecotones. The results also indicate that bison migrated greater distances during climatically warmer periods associated with the spread of woody vegetation.

The information derived from this study has important implications for understanding how prehistoric groups structured their settlement and subsistence patterns, and I argue that there were likely fluctuations on a seasonal basis in site structure and resource procurement behavior, varying between relatively greater logistical mobility in the summer and fall and relatively greater residential mobility in the winter and early spring. Based on changes in the scale of bison mobility during periods of warmer climate, I also argue that logistical mobility may have structured settlement and subsistence patterns to a greater degree during the Late Pleistocene as bison populations were likely relatively less migratory than later periods. However, as climates continued to warm and woody vegetation spread during the Early Holocene, bison populations likely became more fragmentary and mobile, which may have caused a shift towards a more residentially-organized settlement and subsistence pattern and away from a bison as a primary subsistence resource.

Through the course of this analysis, several limitations were noted that can be addressed in future research. Primarily, it will be important to sequentially-sample and analyze steppe bison teeth dating to the Holocene. This will not only provide a better understanding of how human populations may have responded to steppe bison behavior during this period, but will also provide a more complete picture of how bison populations responded to increased spread of woody vegetation during the Holocene, and climate change at a broad scale. Additionally, incorporating specimens from both lowland and upland locations may more fully demonstrate habitat availability through different climatic periods.

This study has also provided some information that goes beyond the initial goals stated in Chapter 1. First, strontium appears to be a reliable method for reconstructing the behavioral ecology of prehistoric species, even considering issues with $^{87}Sr/^{86}Sr$ fluctuation in permafrost regions (i.e., Douglas et al. 2013). Second, steppe bison behavior appears to more closely reflect the behavior of modern wood bison rather than plains bison behavior in terms of both diet and seasonal mobility patterns (this idea was also presented by Rivals et al. [2007, 2010]), which suggests that wood bison are a more accurate analog for modeling future reconstructions of steppe bison behavioral ecology. Third, contrary to Guthrie's (1990) hypothesis about high degrees of mobility, steppe bison do not appear to have been highly mobile, and even during temporally-warm periods when mobility increased, changes in geographical location appear to have occurred on a scale of >700 km^2. Fourth, the data are strongly indicative that climate change was a driving factor behind the eventual extinction of steppe bison. Although future studies will be needed to validate this, this study provides one of the first empirical demonstrations that the spread of woody vegetation likely fragmented bison habitat, forcing them to migrate greater distances between forage patches. Fifth, this study suggests that

reconstructions of animal behavioral ecology do not capture the full range of behavior when they only are focused on constrained temporal periods (e.g. Britton et al. 2011; Juliens et al. 2012), and that studies focused on a limited time-period should only be used to model animal behavior in context of that temporal period. Finally, weather patterns throughout the last 35,000 years of the Pleistocene appear to have been very dynamic, and temperature, precipitation, seasonality, and the timing of peak warm and cool seasons appears to have fluctuated to a large degree, based on the $\delta^{18}O$ patterns. While the purpose of this study was not to reconstruct climate patterns, the results suggest that it is possible to reconstruct past climate patterns on a seasonal basis by sequentially-sampling ungulate teeth, and future studies of a similar nature have the potential to reconstruct the types of weather patterns that Beringia experienced during the Pleistocene.

In closing, the results of this study not only help us to understand the human past, but it can also inform on the present. Now more than ever, understanding the mechanisms driving species decline and extinctions is essential. All ecosystems are composed of a web of integrated components, and modern studies are only beginning to reveal the complexity of those relationships. Limited as paleo-reconstructions are, studies such as this one that focus on regional-scale reconstructions can address spatial and temporal patterns that are not evident in modern systems or accessible through other means. As more research contributes to our understanding of global climate change both past and present, we can begin to reconstruct how these changes affected plant and animal communities, and begin to understand the cause-and-effect processes associated with climate change at a broader scale.

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- APPENDICES -

APPENDIX A: Raw Isotope Values for Modern Samples

Strontium isotopes analyzed at the Strontium Isotope Geochemistry Laboratory, University of Utah, Salt Lake and calibrated using SRM987. Oxygen and carbon isotopes analyzed at the Alaska Stable Isotope Facility, University of Alaska, Fairbanks, and reported relative to Standard Mean Ocean Water and Vienna Pee Dee Belemnite, respectively. Error values represent standard reported error.

Isotope Values for Modern Delta Herd Samples							
Sample ID	**Distance from CEJ**	**$^{87}Sr/^{86}Sr$**	**$^{87}Sr/^{86}Sr$ Error**	**$\delta^{18}O$**	**$\delta^{18}O$ Error**	**$\delta^{13}C$**	**$\delta^{13}C$ Error**
DH1a-1	30.2	0.71556	0.00002	-17.8	0.2	-14.3	0.3
DH1a-2	26.2	0.71584	0.00002	-17.4	0.2	-14.3	0.2
DH1a-3	22.3	0.71599	0.00001	-17.6	0.2	-14.5	0.2
DH1a-4	18.5	0.71626	0.00002	-18.0	0.1	-14.6	0.2
DH1a-5	14.9	0.71622	0.00002	-18.8	0.2	-14.8	0.2
DH1a-6	11.7	0.71591	0.00002	-19.3	0.1	-14.8	0.2
DH1a-7	7.9	0.71562	0.00002	-20.2	0.2	-14.9	0.2
DH1a-8	3.4	0.71525	0.00002	-20.7	0.2	-14.8	0.2
DH1b-1	32.2	0.71542	0.00002	-20.6	0.2	-14.7	0.2
DH1b-2	28.7	0.71544	0.00002	-20.4	0.2	-14.8	0.2
DH1b-3	24.7	0.71569	0.00002	-20.3	0.2	-14.8	0.2
DH1b-4	20.4	0.71579	0.00002	-19.7	0.2	-14.5	0.2
DH1b-5	16.3	0.71607	0.00002	-18.6	0.2	-14.5	0.2
DH1b-6	12.5	0.71633	0.00002	-18.3	0.2	-14.5	0.2
DH1b-7	8.6	0.71628	0.00002	-18.4	0.1	-14.4	0.1
DH1b-8	3.8	0.71620	0.00002	-19.1	0.2	-14.4	0.2
DH2-1	44.8	0.71612	0.00002	-19.6	0.2	-15.2	0.2
DH2-2	40.3	0.71584	0.00002	-20.2	0.1	-15.0	0.1
DH2-3	36.6	0.71608	0.00002	-20.5	0.1	-15.0	0.1
DH2-4	32.4	0.71609	0.00001	-20.3	0.1	-14.9	0.2
DH2-5	28.5	0.71617	0.00002	-20.3	0.2	-15.9	1.1
DH2-6	24.5	0.71624	0.00002	-20.1	0.2	-14.8	0.1
DH2-7	20.3	0.71642	0.00002	-19.3	0.1	-14.7	0.1
DH2-8	16.7	0.71683	0.00002	-18.9	0.2	-14.6	0.1
DH2-9	12.9	0.71711	0.00003	-18.7	0.2	-14.7	0.1
DH2-10	8.9	0.71679	0.00002	-18.9	0.2	-14.9	0.1
DH2-11	3.9	0.71639	0.00002	-20.0	0.2	-14.7	0.1

APPENDIX B: Raw Isotope Values of Prehistoric Samples

Strontium isotopes analyzed at the Strontium Isotope Geochemistry Laboratory, University of Utah, Salt Lake and calibrated using SRM987. Oxygen and carbon isotopes analyzed at the Alaska Stable Isotope Facility, University of Alaska, Fairbanks, and reported relative to Standard Mean Ocean Water and Vienna Pee Dee Belemnite, respectively. Error values represent standard reported error.

Isotope Values for Prehistoric Samples								
Sample	**Distance from CEJ (mm)**	**rcyBP**	**$^{87}Sr/^{86}Sr$**	**$^{87}Sr/^{86}Sr$ Error**	**$\delta^{18}O$**	**$\delta^{18}O$ Error**	**$\delta^{13}C$**	**$\delta^{13}C$ Error**
6335-1	29.3	12840 ±30	0.71080	0.00003	-22.3	0.2	-11.1	0.1
6335-2	25.8	12840 ±30	0.71081	0.00004	-22.4	0.2	-11.2	0.1
6335-3	21.7	12840 ±30	0.71072	0.00003	-22.2	0.2	-11.2	0.2
6335-4	18.3	12840 ±30	0.71046	0.00002	-21.7	0.2	-11.2	0.2
6335-5	13.6	12840 ±30	0.71029	0.00001	-20.3	0.1	-11.5	0.1
6335-6	9.9	12840 ±30	0.70983	0.00001	-20.5	0.2	-11.7	0.2
6335-7	5.6	12840 ±30	0.70943	0.00001	-20.3	0.1	-11.4	0.1
6335-8	2.2	12840 ±30	0.70908	0.00001	-21.4	0.2	-11.3	0.1
FPT	24.2	14280 ±230	0.71247	0.00001	-16.5	0.2	-10.6	0.2
FPT-2	21.8	14280 ±230	0.71236	0.00000	-16.3	0.2	-10.5	0.2
FPT-3	18	14280 ±230	0.71238	0.00001	-15.9	0.2	-10.3	0.2
FPT-4	13.7	14280 ±230	0.71241	0.00001	-16.2	0.2	-10.0	0.2
FPT-5	9.8	14280 ±230	0.71242	0.00001	-16.9	0.2	-10.2	0.2
FPT-6	5.7	14280 ±230	0.71245	0.00001	-18.2	0.3	-9.9	0.3
6173-1	35.4	17360 ±50	0.71111	0.00001	-19.7	0.2	-11.4	0.2
6173-2	31.4	17360 ±50	0.71110	0.00001	-19.5	0.2	-11.2	0.2
6173-3	26.2	17360 ±50	0.71108	0.00001	-19.3	0.2	-11.0	0.2
6173-4	22	17360 ±50	0.71106	0.00001	-20.0	0.2	-11.0	0.2
6173-5	18.2	17360 ±50	0.71107	0.00001	-20.3	0.2	-11.1	0.1
6173-6	15.1	17360 ±50	0.71106	0.00001	-20.4	0.1	-10.9	0.1
6173-7	8.3	17360 ±50	0.71115	0.00001	-20.7	0.2	-10.9	0.2
6173-8	4.9	17360 ±50	0.71123	0.00001	-20.8	0.2	-10.5	0.1
6768-1	29.2	18940 ±50	0.70926	0.00004	-20.2	0.2	-10.1	0.1
6768-2	25.9	18940 ±50	0.70921	0.00003	-19.7	0.1	-9.9	0.1
6768-3	21.3	18940 ±50	0.70923	0.00001	-19.6	0.2	-9.8	0.1
6768-4	18.5	18940 ±50	0.70912	0.00001	-19.7	0.2	-10.0	0.1
6768-5	14.1	18940 ±50	0.70909	0.00001	-19.4	0.2	-9.9	0.1
6768-6	10.9	18940 ±50	0.70922	0.00002	-19.3	0.2	-9.7	0.2
6768-7	6.4	18940 ±50	0.70914	0.00002	-19.7	0.2	-9.7	0.1
6768-8	2.9	18940 ±50	0.70914	0.00002	-19.3	0.2	-9.3	0.1

Sample	Distance from CEJ (mm)	rcyBP	$^{87}Sr/^{86}Sr$	$^{87}Sr/^{86}Sr$ Error	$\delta^{18}O$	$\delta^{18}O$ Error	$\delta^{13}C$	$\delta^{13}C$ Error
6377-1	42.8	27950 ±90	0.71274	0.00001	-19.6	0.2	-10.1	0.2
6377-2	35.9	27950 ±90	0.71271	0.00001	-20.2	0.2	-10.2	0.1
6377-3	34.8	27950 ±90	0.71265	0.00002	-20.6	0.2	-10.1	0.1
6377-4	32.1	27950 ±90	0.71259	0.00002	-20.5	0.2	-10.2	0.1
6377-5	27.8	27950 ±90	0.71259	0.00002	-20.7	0.2	-10.2	0.1
6377-6	23.3	27950 ±90	0.71276	0.00001	-20.4	0.2	-10.1	0.2
6377-7	19.6	27950 ±90	0.71297	0.00001	-19.7	0.2	-10.1	0.1
6377-8	16.2	27950 ±90	0.71333	0.00001	-18.9	0.2	-10.1	0.1
6377-9	11.9	27950 ±90	0.71341	0.00001	-18.3	0.2	-10.3	0.1
6377-10	8.5	27950 ±90	0.71386	0.00001	-19.3	0.2	-10.1	0.1
6377-11	5.1	27950 ±90	0.71367	0.00001	-19.9	0.1	-10.1	0.1
6602-1	31.5	29390 ±100	0.70825	0.00001	-22.4	0.2	-9.9	0.2
6602-2	26.6	29390 ±100	0.70827	0.00001	-22.4	0.2	-10.0	0.1
6602-3	23.3	29390 ±100	0.70827	0.00002	-22.4	0.2	-10.1	0.1
6602-4	19.6	29390 ±100	0.70821	0.00001	-21.9	0.2	-10.2	0.1
6602-5	15.2	29390 ±100	0.70815	0.00002	-21.5	0.2	-10.2	0.1
6602-6	10.4	29390 ±100	0.70813	0.00002	-22.0	0.2	-10.5	0.2
6602-7	6.1	29390 ±100	0.70817	0.00002	-21.9	0.2	-10.4	0.1
6602-8	1.9	29390 ±100	0.70842	0.00002	-22.7	0.2	-10.1	0.1
6620-1	37.7	30810 ±110	0.70833	0.00002	-20.7	0.2	-10.7	0.1
6620-2	32.5	30810 ±110	0.70829	0.00002	-20.2	0.2	-10.7	0.1
6620-3	28.9	30810 ±110	0.70819	0.00001	-20.1	0.2	-10.7	0.1
6620-4	24.9	30810 ±110	0.70812	0.00001	-19.4	0.2	-10.5	0.1
6620-5	20.4	30810 ±110	0.70804	0.00001	-19.5	0.2	-10.3	0.1
6620-6	16.5	30810 ±110	0.70801	0.00001	-19.7	0.2	-10.3	0.1
6620-7	12.2	30810 ±110	0.70799	0.00001	-20.5	0.2	-9.9	0.1
6620-8	8.3	30810 ±110	0.70829	0.00001	-21.2	0.1	-9.7	0.1
6620-9	3.4	30810 ±110	0.70864	0.00001	-21.7	0.2	-9.6	0.1
6616-1	31.8	33420 ±130	0.71097	0.00001	-22.2	0.2	-10.2	0.1
6616-2	28.2	33420 ±130	0.71112	0.00001	-22.1	0.2	-10.3	0.2
6616-3	24.2	33420 ±130	0.71136	0.00001	-21.3	0.2	-10.6	0.1
6616-4	20.4	33420 ±130	0.71180	0.00001	-21.3	0.2	-10.3	0.2
6616-5	16.3	33420 ±130	0.71220	0.00001	-20.8	0.2	-10.5	0.1
6616-6	12.4	33420 ±130	0.71254	0.00001	-20.7	0.2	-10.7	0.2
6616-7	8	33420 ±130	0.71265	0.00001	-20.7	0.2	-10.6	0.1
6616-8	3.9	33420 ±130	0.71224	0.00001	-21.3	0.2	-10.4	0.2
6785-1	28.4	33720 ±120	0.70784	0.00001	-20.6	0.2	-11.3	0.1
6785-2	24.5	33720 ±120	0.70787	0.00001	-20.3	0.2	-11.1	0.2
6785-3	20.4	33720 ±120	0.70788	0.00001	-19.9	0.1	-11.1	0.1

Sample	Distance from CEJ (mm)	rcyBP	$^{87}Sr/^{86}Sr$	$^{87}Sr/^{86}Sr$ Error	$\delta^{18}O$	$\delta^{18}O$ Error	$\delta^{13}C$	$\delta^{13}C$ Error
6785-4	16.2	33720 ±120	0.70788	0.00001	-19.8	0.2	-11.4	0.1
6785-5	12.4	33720 ±120	0.70783	0.00001	-19.4	0.2	-11.1	0.1
6785-6	8.3	33720 ±120	0.70788	0.00001	-19.0	0.2	-10.9	0.1
6785-7	4.6	33720 ±120	0.70790	0.00001	-19.3	0.2	-10.7	0.1
12224-1	24.2	34070 ±140	0.70687	0.00002	-20.0	0.1	-11.3	0.1
12224-2	21.8	34070 ±140	0.70671	0.00002	-20.1	0.2	-11.0	0.2
12224-3	18	34070 ±140	0.70678	0.00002	-20.7	0.1	-11.0	0.1
12224-4	13.7	34070 ±140	0.70688	0.00002	-21.2	0.2	-11.1	0.1
12224-5	9.8	34070 ±140	0.70704	0.00002	-21.9	0.1	-10.8	0.1
12224-6	5.7	34070 ±140	0.70720	0.00002	-21.7	0.2	-10.8	0.1
6382-1	23.7	41400 ±220	0.70792	0.00001	-21.1	0.4	-11.2	0.2
6382-2	19.7	41400 ±220	0.70785	0.00001	-20.7	0.4	-11.3	0.3
6382-3	14.7	41400 ±220	0.70780	0.00001	-20.1	0.3	-11.2	0.3
6382-4	12	41400 ±220	0.70774	0.00001	-20.1	0.2	-11.3	0.2
6382-5	7.4	41400 ±220	0.70775	0.00001	-21.1	0.3	-11.4	0.2
6382-6	4.3	41400 ±220	0.70796	0.00001	-20.5	0.2	-11.7	0.2
8582-1	21.6	43370 ±300	0.71043	0.00002	-20.9	0.2	-11.1	0.1
8582-2	18.5	43370 ±300	0.71032	0.00001	-20.7	0.2	-11.1	0.1
8582-3	14.7	43370 ±300	0.71028	0.00002	-20.8	0.1	-11.0	0.1
8582-4	11	43370 ±300	0.71025	0.00002	-21.4	0.2	-10.9	0.1
8582-5	7	43370 ±300	0.71041	0.00003	-22.0	0.2	-11.0	0.1
8582-6	3.2	43370 ±300	0.71043	0.00003	-22.0	0.1	-10.9	0.1
6594-1	29.4	47290 ±500	0.70959	0.00001	-21.5	0.2	-11.6	0.2
6594-2	25.7	47290 ±500	0.70959	0.00001	-21.2	0.1	-11.7	0.2
6594-3	22.2	47290 ±500	0.70963	0.00001	-20.4	0.2	-12.0	0.2
6594-4	18	47290 ±500	0.70964	0.00001	-20.7	0.2	-12.0	0.1
6594-5	14.9	47290 ±500	0.70964	0.00001	-21.3	0.2	-11.9	0.2
6594-6	11.1	47290 ±500	0.70969	0.00001	-22.1	0.1	-11.8	0.1
6594-7	7.1	47290 ±500	0.70971	0.00001	-22.4	0.2	-11.7	0.1
6594-8	3.7	47290 ±500	0.70982	0.00001	-22.6	0.1	-11.4	0.1
6599-1	26.5	>51550	0.70885	0.00001	-21.6	0.1	-11.0	0.1
6599-2	22.6	>51550	0.70891	0.00001	-20.7	0.1	-11.2	0.1
6599-3	17.4	>51550	0.70888	0.00001	-20.1	0.2	-11.3	0.1
6599-4	13.5	>51550	0.70890	0.00001	-18.4	0.2	-8.5	0.1
6599-5	10.2	>51550	0.70887	0.00001	-20.4	0.2	-11.2	0.1
6599-6	6.3	>51550	0.70881	0.00001	-20.1	0.2	-11.0	0.2
6599-7	2.6	>51550	0.70878	0.00001	-20.0	0.1	-10.9	0.1

APPENDIX C: Mean strontium values northeast and southwest of the sample locales.

Mean $^{87}Sr/^{86}Sr$ and SD for 180 Degree Arcs Northeast and Southwest of Lost Chicken Creek and The CRREL Permafrost Tunnel.

	Direction	Distance (km)	Mean $^{87}Sr/^{86}Sr$	SD
Lost Chicken Creek	NE	-100	0.70749	0.00195
	NE	-90	0.70805	0.00144
	NE	-80	0.70830	0.00119
	NE	-70	0.70842	0.00128
	NE	-60	0.70826	0.00166
	NE	-50	0.70830	0.00103
	NE	-40	0.70821	0.00044
	NE	-30	0.70805	0.00034
	NE	-20	0.70800	0.00037
	NE	-10	0.70772	0.00019
	NE	-5	0.70754	0.00032
	SW	5	0.70754	0.00032
	SW	10	0.70772	0.00019
	SW	20	0.70800	0.00037
	SW	30	0.70871	0.00058
	SW	40	0.70860	0.00102
	SW	50	0.70835	0.00152
	SW	60	0.70860	0.00239
	SW	70	0.70939	0.00176
	SW	80	0.70998	0.00159
	SW	90	0.71035	0.00171
	SW	100	0.71088	0.00167
	SW	110	0.71207	0.00294
CRREL Permafrost Tunnel	NW	-50	0.71361	0.00208
	NW	-40	0.71301	0.00150
	NW	-30	0.71370	0.00115
	NW	-20	0.71487	0.00211
	NW	-10	0.71760	0.00401
	NW	-5	0.71853	0.00089
	SE	5	0.71853	0.00089
	SE	10	0.71760	0.00401
	SE	20	0.71786	0.00473
	SE	30	0.71813	0.00535
	SE	40	0.71803	0.00452
	SE	50	0.71753	0.00354